THE

CYCLOPÆDIA

OF

ANATOMY AND PHYSIOLOGY.

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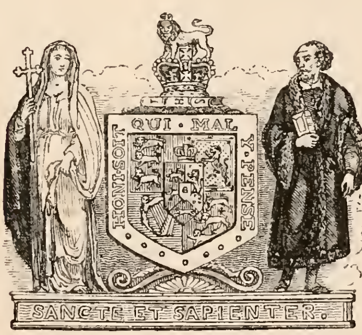

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CONTENTS

OF

THE SUPPLEMENTARY VOLUME.

SUPPLEMENT.

OVUM.—In Animal Anatomy and Physiology, the Egg, the product of parental sexual generation, from which the young of animals are produced.

The Functions of Reproduction, as observed in the higher orders of animals and in the human species, are generally divided into two classes of processes; the one of which comprehends those operations by which the parents contribute to the production of the germs from which the young are formed; the other, those processes or changes which occur more immediately in the product of generation itself, and which relate to the formation or development of the new being from a germ or ovum. In the Article Generation of this Cyclopædia, the functions belonging to the first of these divisions have been described; and it is proposed in the present Article to treat of the second class of reproductive phenomena, or those which relate more immediately to the origin, formation, and growth of the new being, and which are usually described under the titles of Ovology, Embryology, and Fœtal Development.

In this, as in the former article, the history of the functions as they occur in the human species will receive the greatest share of our attention; but in describing the process of development of the young, still more than in the history of the functions of the parents that are preliminary to the production of a perfect germ, it is necessary to extend our observations to the various members of the animal kingdom, and even in some degree also to plants, from which, as much as from direct observations or experiments in man, has been derived our knowledge of the individual facts and of the general laws relating to the process of embryonic development.

The arrangement followed in that part of the article which treats of Development will be adapted more immediately to the consideration of human reproduction; and the statements in regard to animals, or to organised beings in general, will be made chiefly subordinate to, or illustrative of, the functions in the human species; but the facts in human and comparative embryology are so intimately connected, that it will be expedient to incorporate with the article such a description of the formative process in different animals as may present a sketch of the general nature of this interesting process in the whole animal kingdom.*

In pursuing this plan, the topics to be discussed may be arranged under the following heads: viz.—

1st. Nature of the Ovum in general, with reference to the different forms of the reproductive function in various animals.

2nd. The structure, properties, mode of origin, and formation of the Ovum.

3rd. The changes which the ovum undergoes in the process of Fecundation, and (in so far as the ovum itself is concerned) the circumstances which influence that process.

4th. The external circumstances which influence the development of the ovum and embryo, especially Incubation and Utero-gestation.

5th. The Phenomena of Fœtal Development in general, and the history of the origin and development of each system, organ, and texture of the body in particular.

6th. The Functions of the Embryo or Fœtus as compared with those of the adult.

The wide-spread importance of embryological anatomy and physiology is now so generally acknowledged by all who have made them a subject of study, that to them no apology is required for the length of this treatise. To those who have not made them an object of their special attention, it will be enough at this place to advert to the extensive range of topics which must be embraced in an attempt to trace the history of the first origin and subsequent evolution of all the parts of so complex and various a structure as the body of animals; and to remind them that this department of science professes to describe not merely the successive changes of external form and relation by which the several organs, springing from imperceptible beginnings, arrive at their perfect condition, but also the more minute phenomena of histological development, or changes of the several textures, which accompany the more obvious formative processes; that, as in many instances the complete knowledge of

* It was originally intended to have treated in the same article of the embryology of plants; but the extent and importance of that subject in connection with general physiology makes it necessary to postpone its consideration to a separate article, under the head of Vegetable Ovum.

the structure and function of an organ is only to be obtained by the observation of its fœtal conditions, the study of development is accessory or supplementary to many departments of anatomy and physiology; that, in recent times, no branch of inquiry relating to organic nature has made more rapid progress, has presented a greater amount of new discoveries, or has influenced in a greater degree the views of scientific men on allied subjects, than the science of embryology; that it is coextensive with, and illustrative of, the whole range of comparative anatomy; that no system, therefore, of zoological classification can be regarded as philosophical or complete which neglects the facts and principles of fœtal development: finally, that some departments of pathological anatomy receive considerable illustration from our science, and that more especially the scientific study and comprehension of teratology or congenital malformations is founded entirely on an accurate knowledge of the phenomena and laws of development. Our subject, therefore, is not only interesting by itself, but deeply important as an essential branch of philosophical anatomy and physiology.*

Before proceeding with the particular history of the ovum, and its development in man and the higher animals, which will form the greater part of the following article, some topics of a general and preliminary nature present themselves for our consideration.

The investigation of the process of reproduction in the lower animals has made so much progress during the last few years, that it becomes necessary to place before the reader a sketch of the aspect in which more modern researches enable the physiologist to view the relation of the ovum to the sexual generative function, and to the other means by which individuals are multiplied, or species are reproduced in the whole animal kingdom. In the Article GENERATION, the commonly received distinction was drawn between the sexual and the non-sexual modes of generation; and under the latter form a variety of processes of Gemmation and Division were alluded to as occasional or constant substitutes in a certain number of animals for the more permanent sexual form of the reproductive process. At the time of the publication of that article, the sexual organs had not been discovered in a considerable number of the lower animals: but since then, the assiduous and accurate researches of embryologists have gradually diminished the number of animals so situated, by bringing to light the male and female reproductive organs, or their essential products, in nearly every species of the animal kingdom; so that now only a very few, and those of the simplest organisation, remain, in which the bisexual condition has not been detected. These animals belong exclusively to the division of the animal kingdom recently established by Zoologists, as Protozoa, comprehending the Polygastric Infusoria, Rhizopoda and Porifera.*

In all other animals it is now ascertained that fecundated ova, formed by an act of sexual generation, are the means of securing the permanent reproduction of the species; but in several of them, as is especially well known among the Polypine tribes, a vast multiplication of individuals, sometimes living separately, but more frequently associated in groups, or living in united colonies, takes place by a non-sexual process of reproduction, which may be compared in many instances to the growth or repetition of the parts of a tree or plant by budding.

Recent investigations have made it more and more apparent, that the non-sexual multiplication of animals ought to be distinguished into several kinds, according to the different circumstances in which it may occur. In a few, as already remarked, it is entirely without known sex: in others, the non-sexual process of gemmation, or division, gives rise to new individuals, which are simply the repetitions of the perfect or complete animals; and in a third set, the non-sexual multiplication occurs more frequently in an incomplete condition of the animal, and often consists in the production of one or more series of dissimilar forms of animals, the last generation of which alone becomes sexually complete, and propagates the species by fecundated ova. This constitutes the variety of the reproductive process recently distinguished by the name of Alternating Generation.

Three forms, therefore, of non-sexual animal reproduction, or multiplication, are to be distinguished from the sexual mode of generation, as in the following enumeration:—

I. True sexual generation, direct or indirect, in all animals, excepting the Protozoa.

II. Non-sexual multiplication, occurring only in some of the invertebrated animals;

1st. In Protozoa, in which sexual organs have not yet been discovered.

* A variety of circumstances have contributed to cause delay in the appearance of the present article, some of them of a nature beyond the control of the author. He is sensible, however; that an apology is due by him to the readers of this work on account of the protraction of that delay. He has only to say, that in the contemplation of the vastness and imperfectly known condition of the subject, he has ever felt more disposed to engage in the investigation of some of its details, than to appear before the public as a systematic writer in regard to it. The delay may have this advantage, however, that it will enable him to introduce a greater number of new discoveries, a more accurate statement of individual facts, and more correct and extended general views of the subject than might have been possible at an earlier period, and that it will afford him an opportunity of correcting and amplifying various statements contained in the previous Article GENERATION, which the progress of discovery since the time of its publication has rendered necessary.

* The first two of these divisions may be described as simple unicellular microscopic animalcules, the third rather as a compound or congeries of microscopic animalcules: the Porifera, or Sponges, are included in this division of Protozoa, because the balance of evidence is decidedly in favour of their animal nature.

2nd. In Animals known to be capable of sexual generation; including two varieties, viz.

a. Multiplication of similar individuals, either in a mature or immature condition.

b. Multiplication of individuals, generally dissimilar from those producing them, and becoming at last mature or complete in the exercise of the true generative function.

Some account of these various forms of the reproductive process, and especially of the last, as established by recent discovery, supplementary to that contained in the Article Generation, may be introduced here, with a view to serve as a foundation for general views of the nature of the ovum, and its relation to the reproductive process in general.

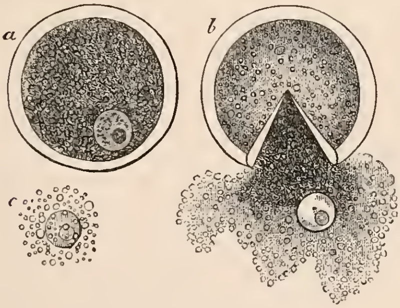
I. Of the Ovum in general, as related to the sexual Process of Generation.

The term *ovum* is in this article entirely restricted to the product of sexual generation. This body is formed in the ovary of the female parent (or in the female organ of a hermaphrodite parent) by a gradual process of growth or development. When it arrives at a state of maturity, it is spontaneously discharged from the place of its formation, a process which in the higher animals has received the name of *Ovulation.* If left to its own unassisted powers, no organic change of importance follows in the ovum, and it remains incapable of producing an embryo. But if, at or near the time when the ovum, in a state of maturity, leaves the ovary, it be subjected to the influence of the male product or sperm by the contact of a very minute portion of that substance, it then undergoes the change of Fecundation, by which it has communicated to it the power of having developed within it a new being specifically resembling its parents.

Although there are many great apparent differences in the form and structure of the ova of animals*, yet a general comparison of their organisation shows that they consist in nearly all of parts that are essentially the same. These parts in the ovarian ovum are the following, beginning with that which appears most essential: 1st, The *Germinal Vesicle*, or *Germ-cell;* a nucleated organic cell of microscopic size, generally situated near the surface of the ripe ovarian ovum: this is embedded superficially in, 2nd, The *Vitellus*, *Yelk*, or *Yolk*, a mass of oleo-albuminous matter, partly fluid, and partly cellular and granular, generally of proportionally much greater size than the germ-cell, and serving to furnish materials for the changes of that body, and for the development of the new being. Both of these parts are enclosed by, 3rd, The *Vitelline*, or *Yolk-Membrane*, a vesicular, nearly structureless, membrane, which contains the rest, and gives to the whole usually more or less of a spherical form. To the assemblage of these parts, constituting the ovarian ovum, and which may be looked upon as most immediately important in connection with the formative process, there are generally added, after it has left the ovary, and in the progress of its descent through the female passages, some others, such as the albumen, outer membrane and shell of the bird's egg. In their simplest form these additional parts constitute an external covering of the egg, to which the name of *Chorion* is often applied.

If the ovum be traced back to its earliest origin in the ovary, it is found to consist at first of the germinal vesicle, germ-cell or its nucleus (*fig.* 1, c.). To this cell the substance of the yolk is added in the progress of its formation, generally in a gradual manner, but in some animals more suddenly.

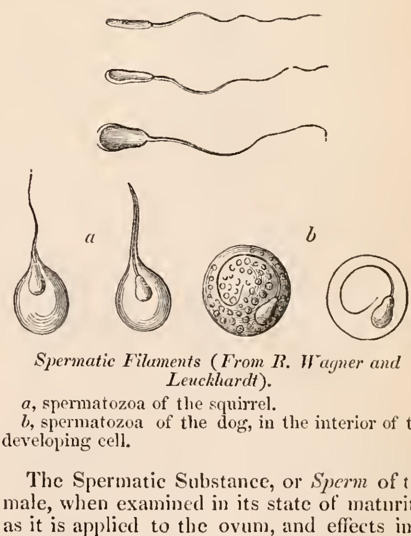
Fig. 1.



Ovarian Ovum of a Mammifer.

a, entire; *b*, burst, showing the germ-cell, with yolk granules flowing out of the vitelline membrane; *c*, the ovarian ovum at an early stage of its formation, consisting of the germ-cell surrounded by a few yolk granules.

Fig. 2.



Spermatic Filaments (From R. Wagner and Leuckhardt).

a, spermatozoa of the squirrel.
b, spermatozoa of the dog, in the interior of the developing cell.

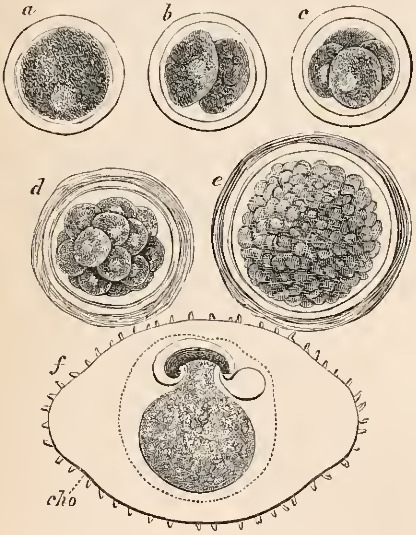
The Spermatic Substance, or *Sperm* of the male, when examined in its state of maturity, as it is applied to the ovum, and effects in it the peculiar change of fecundation, is observed to consist essentially of an immense number of minute bodies, generally consisting of a thicker particle, with a fine filament attached,

* The most important of these will be noticed in a later part of the article.

and almost always exhibiting, when recently mixed with water, vivid vibratory or undulatory movements, but in a few animals presenting other forms, and without motion. These spermatic filaments or particles are developed by a peculiar process in the interior of the cells (*sperm-cells*) secreted in the male organ or testis.

When the ovarian ovum has arrived at maturity, the germ cell disappears as such, and if fecundation shall have taken place, that vesicle is succeeded by another minute cell, with which the origin and development of the new animal are most intimately associated. This secondary organic cell of the fecundated ovum has therefore been called the *Embryo-cell.* The first changes, preparatory to the commencement of the development of an embryo, consist in the formation out of the embryo-cell and yolk substance of an organised cellular mass, or of a membranous covering of the whole or a part of the yolk: this is the *germ-mass*, *Blastoderm*, or *germinal membrane.*

Fig. 3.



Fecundated Ovum of a Mammifer, with the Embryo Cell and its division.

a, ovum with the first embryo-cell ; *b*, division of embryo-cell and cleavage of the yolk round it ; *c*, second division and cleavage ; *d*, farther division ; and *e*, germ-mass or Blastoderm forming ; *f*, diagram of the embryo with its membranes, the amnion, allantois, &c., within the chorion.

The process by which this primary organised part is produced varies somewhat in different animals; but it appears to consist in a multiplication of the embryo-cell by changes of the nature of cytogenesis, accompanied with more or less of a cleavage or sub-division of the substance of the yolk, and its combination with the progeny of the embryo-cell. The general result is, that the first rudiments of the new being take their origin in organic cells, which are descended from the original embryo-cell.

From this blastodermic mass or membrane, the embryo, or fœtus, or new animal, and in the higher animals some accessory parts, which are temporarily united with the embryo previous to its birth, originate, and are gradually formed, by a various process of progressive organic growth of an epigenetic character, which is termed *Development*, or *Embryo-genesis.*

In by far the greater number of animals an ovum gives rise to only one embryo or individual, and this one becomes by itself, when its growth is complete, the perfect sexual animal, capable of contributing its share to the production of fecundated ova. But in a certain number of animals, to which allusion will be made more fully afterwards, the immediate product of development from the ovum is not at once, and by itself, converted into a complete sexual individual; but by an intermediate non-sexual process of production, one or more new individuals are formed out of the body of that first developed, and to the last so formed is committed the office of sexual reproduction, or true generation.

The essential conditions and phenomena, therefore, of the sexual process of generation, as related to the ovum, and as limited by the foregoing considerations, may be shortly stated to be the following:—

1st. The formation of the ovarian ovum of the female sex, containing the germ-cell.

2nd. The formation of the sperm-cells of the male sex, and the development of their peculiar spermatic elements.

3rd. The mutual action of these two products in the fecundation of the ovum.

4th. The disappearance of the germ-cell of the ovarian ovum, and the formation of the embryo-cell in the fecundated egg.

5th. The multiplication of the embryo-cell by cytogenesis, and the formation from that body, and from the yolk, or a part of it, of the blastodermic mass or membrane.

6th. The process of embryo-genesis, or development of the systems, organs, and textures of the new animal.

It is right to state that the original germ-cell has not yet been ascertained to exist in the ovum of every animal, nor has its successor, the embryo-cell, been observed in all instances; but they have been detected in so very large a proportion, that it appears extremely probable that in all sexual animals the generative process consists in the process above described, or in some modification of it. I refrain at present from farther details as to these phenomena, and have stated the results only in their most general form, because I shall have occasion to return upon some of them in a subsequent part of the article. Looking back on this general statement of the commencement and progress of the genetic process in animals, it will be seen that the new being may be considered as taking its immediate origin from the progeny of cells descended from the embryo-cell. That cell appears with great probability to take its origin from the germ-cell, or its nucleus, or from some part of it, in combination with a determinate portion of the sperm product, or descendent of the sperm-cell; and we are so far justified, therefore, in ascribing the genetic process by which the new being is formed to the mutual action of the products of two different kinds of cells, viz., the germ-cell and the sperm-cell.*

In conclusion, the ovum may be defined to be a distinct vesicular body originally formed from a cell, presenting throughout its existence the organic cellular structure, consisting of oleo-albuminous materials, formed by the female of an animal species, and capable, when acted on by the spermatic product of the male, of undergoing the successive changes of embryo-genesis, by which, either directly or through intervening generations, the species of animals is reproduced and continued.

The structural distinctive characters of an ovum are, therefore, its enclosure within a distinct vesicular covering, and its original organic cellular constitution in the germ-cell: its most important physiological characteristic is its susceptibility of the changes of embryonic development under the influence of the sperm-cell or its product.

II. Of the non-sexual Mode of Generation.

The necessity of distinguishing several kinds of non-sexual reproduction according to its occurrence in animals entirely without sex, or believed to be so, and in those which may also be propagated in the sexual mode, has already been adverted to. A farther distinction of the non-sexual reproduction may be made according to the nature of the process itself: thus, some forms of it consist in the development of buds, so intimately united with the parent substance, that scarcely any difference can be perceived between their mode of formation and that of continuous growth, as in Hydra and various Polypes: other forms consist in the development of new individuals from germs so isolated in their form and cellular in their structure, that it might seem at first sight arbitrary to distinguish them from ova, as in Aphides; others appear to hold an intermediate place and character between these two forms, as in Salpa: while, in a fourth set, a more complex and varied series of changes occurs, which may be regarded with probability as modifications of the gemmal or germinal processes, as in Medusoid Polypi, Taenia, &c. But it will be apparent from what follows that we are as yet very far from that exact knowledge of the nature and first origin of buds, gemmæ, or other kinds of germs, from which animals may be multiplied in the non-sexual modes, which would enable us to form satisfactory general conclusions as to their mutual relations, and their similarity or difference, as compared on the one hand with organic growth, and on the other with oval development.

As the accurate determination of these relations is in a great measure impossible, it will be expedient for the present to state only very briefly the general characters of the several non-sexual modes of reproduction, before selecting for more particular consideration some varieties of the process, the recent investigation of which seems calculated to influence in a considerable degree future general views of the whole subject of reproduction. We shall also defer for the present any minute consideration of the relation of these processes to the growth or development of cells, for we shall have occasion to treat more at length of that subject in a subsequent part of this article, and in that of vegetable ovum.*

At this place it is only necessary to remind the reader, that all processes of development, whether in the earliest or at more advanced stages of formation, appear to consist essentially in, or are more or less intimately connected with, a multiplication of organic cells in the parts that are developed. In the unicellular beings, fissiparous and gemmiparous multiplication may easily be recognised to be processes of cell growth; the one consisting in the division of the parent cell into a progeny of two by a nearly equal partition of its substance; the other, in an extension and gradual enlargement of a small or limited portion of the original cell. But in many of the instances of fission and gemmation on the larger scale with which we are acquainted, observation has not yet pointed out the primary cell, if it exists, from which the process of division or extension begins; and, indeed, most instances of fissiparous division may, as Dr. Carpenter has remarked, be referred to a peculiar modification of gemmation.

The process of budding or gemmation is usually stated to occur in one of two modes. 1st, by the extension of a part of the parent body which remains in organic connection with it during the development of the new individual from the bud; the attached bud either sprouting from the exterior, or being developed in the interior of the parent stock. 2nd, by the development of the new individual from a small detached portion of the substance of the parent, which undergoes the principal formative changes after its separation. These separate buds have been called gemmae, gemmules, bulbils, &c., and two kinds of them may also be distinguished according as they are thrown off from the external surface of the parent body, or are formed and become loose within its interior. These gemmules have frequently attained to some degree of development by the time of their separation, and very often are provided with cilia over their surface, which cause them to move

* These views have been stated with great clearness by Prof. Owen in his various writings, especially in his Essay on Parthenogenesis, and Lectures on Generation, &c., in Medical Times, 1849, and by Dr. Carpenter in his Principles of Physiology, General and Comparative. 1851.

* For a very lucid and agreeable statement of these relations the reader is referred to Dr. Carpenter's able Treatise on General and Comparative Physiology. 1851.

rapidly through fluids. From the first they exhibit a minutely cellular and granular structure: but it does not appear that they are originally formed from any single nucleated cell: they appear rather from the first to be a congeries of cell progenies. They are destitute of an external envelope; but, nevertheless, it may often be difficult to distinguish between them and true ova.

The tendency to the multiplication of individuals by non-sexual reproduction is greatest among those animals which are of the simplest organisation, and more especially among those in which the cellular structure predominates; not that it is confined to them, nor that it occurs in all animals so constituted, but that it is much more frequent and complete in the simplest animals of each class in which it has been observed; as if it were more liable to occur in those species in which the process of individual development had proceeded to the least extent of advancement in the formation of the living textures of their bodies. There is accordingly a remarkable similarity in the nature of the processes of non-sexual multiplication and ordinary growth in these very simple animals; and it is well known that the same relation subsists between a low organisation of animals, and their disposition or power to repair individual parts of their bodies lost by injury or accident.*

1st. *Of the Process of Reproduction in Protozoa, or animals in which the sexual distinction has not yet been discovered.*

Among the Protozoa reproduction takes place in two modes, viz., 1st, by the process of gemmation or fission, and, 2nd, by development from separated gemmules or germs. For an account of the first of these processes, the reader is referred to the articles POLYGASTRIA and PORIFERA.†

Among the Polygastria multiplication by division is much more frequent than that by gemmation. It consists in the fission or division of the whole unicellular body into two nearly equal parts, each of which becomes, when separate, a perfect animalcule like the original one: in some the division is transverse, in others longitudinal, and occasionally it occurs in either of these modes in different individuals of the same species. The nucleus of the unicellular polygastria has been frequently observed to undergo division previous to the formation of the fissure, by which the division of the external wall is completed,— a fact which has led some physiologists, as Ehrenberg, M. Barry, and Owen, to attribute to the nucleus an important influence in this process of cleavage; the first of these observers having even conceived the nucleus to act the part of a male or fecundating organ. This latter view is not, however, adopted by many of those who have made a study of this class of animals.

In some of the polygastria in which the process of multiplication is either of a fissiparous or gemmiparous kind, as in Vorticella, Uvella, and Polythalamous Rhizopoda, the new individuals remain in connection, and are associated together in branched pediculated groups, in connected masses of a globular form, or in regular spiral united series.*

The Porifera, or sponges, appear to be reproduced by a different kind of gemmation from that now described in polygastria,—viz., by separate gemmules or small portions of the substance of the sponge, which, soon after having been detached from the main stock, are moulded into a spherical form, and, being provided with cilia, move about in the water with great vivacity for a considerable period. These gemmules are thrown off in numbers proportional in some measure to the activity of the nutrition of the sponge, and therefore principally during the early part of summer. Towards the approach of winter a different kind of reproductive bodies is observed to be formed,— viz. small capsules containing globular germs, which, after development within the capsule, pass out of it and produce a new sponge for every capsule or germ. These bodies have been called ova, and certainly they bear very great resemblance to them; but too little is known of their nature and origin to enable us to form an opinion whether they are to be regarded as precisely of the same nature as ova or not. In the mean time they may be named the capsular germs.†

But it appears that, among the polygastria, and rhizopoda also, there are sometimes formed, by a peculiar process not ascertained to be of a sexual kind, minute reproductive bodies of a cellular structure, which, if they are not true ova, are at least substitutes for them.‡

* See Mr. Paget's recent interesting lectures on this subject, published in Medical Gazette, 1849.

† A considerable number of the polygastric infusoria described by Ehrenberg in his great work on that class, are now very generally regarded as belonging to the vegetable rather than to the animal kingdom, such as the families Closterina, Volvocina, and Bacillaria.

* See an interesting paper by Dr. Carpenter on the Genus Nummulina and other Foraminifera in Quart. Journ. of Geol. Soc. Feb. 1850. Some judicious and interesting remarks on this class of animals, and on the relations and characters of the Protozoa in general, are contained in a recent paper by Mr. Huxley in the Annals of Natural History (1851, vol. viii. p. 437.), in which he has described a curious monocellular genus named Thalassicolla, which occurs in masses, and forms spicula somewhat like a minute sponge.

† See Laurent's elegant memoir, Recherches sur l'Hydre et l'Eponge d'eau douce. 1842.

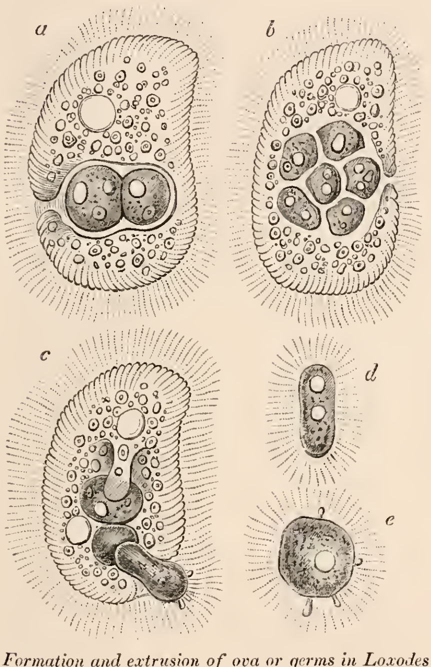
‡ Allusion is not made here to the production of granules by the diffluence of an infusorian animalcule erroneously taken by Ehrenberg for the deposition of ova, but to a very different process. Dujardin, who pointed out this error (Hist. Nat. des Infusoires, p. 101.), is of opinion that, besides the processes of fission and gemmation, we know nothing with certainty of the reproduction of infusoria; but he admits that it is possible that the minute bodies into which an infusorian breaks up by diffluence might prove the germs of new individuals. Dr. Carpenter has mentioned several instances of a kind similar to those alluded to in the text, and has expressed the opinion that something of the nature of sexual production may yet be discovered to take place in these animals (Prin. of Gen. and Comp. Physiol. p. 249, and p. 917.). Observations of a similar kind are re-

Some recent observations appear to throw additional light on this subject, and to make it probable that in some circumstances this process is in some sort analogous, or at least equivalent, to one of sexual reproduction.

The first accurate observation of the development of a progeny of young cells within the body of a polygastrian was communicated by Focke in 1844 to the meeting of naturalists at Bremen, and the fact of the production of internal germs or bodies resembling ova or spores within the body of these animalcules has recently received full confirmation from the observations of Stein and of Cohn.*

In Cohn's observations, which were made on a paramaecian polygastrian, the Loxodes

Fig. 4.



Formation and extrusion of ova or germs in Loxodes bursaria (from Cohn).

a, animalcule, containing two young; *b*, containing six; *c*, one of the embryos escaping; *d*, *e*, two ciliated embryos.

bursaria, which is usually multiplied like the rest, in the fissiparous mode, sometimes by longitudinal, at others, by transverse division, it was found that at certain periods there were formed within the bodies finely granular colourless cells, in some only one, more frequently several, and occasionally as many as six or seven, nearly of a uniform size, and

ferred to under the head of 'sporiferous reproduction,' by Prof. Rymer Jones, in the article POLYGASTRIA.

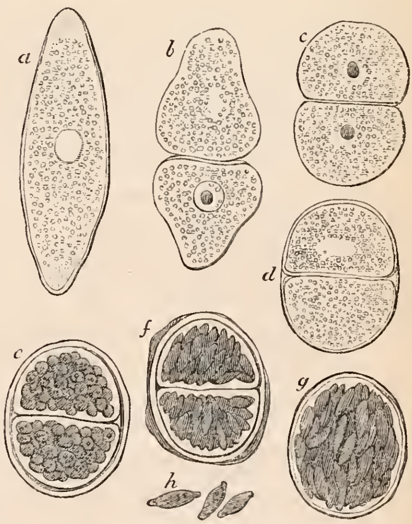
* Stein, Untersuch. üb. die Entwick. der Infusorien, Wiegmann's Archiv., 1849, vol. I. p. 134. in Actinophrys, Acineta, and Chilodon uncinatus. Cohn, in Zeitsch. für Wissensch. Zoologie, Nov. 1851, p. 257.

each presenting two contractile vesicles like the parent. The escape of these bodies, by their passage through an aperture temporarily formed in the wall of the infusorian, was carefully observed; the exit of each embryo occupied about twenty minutes. Soon after their escape they exhibited active ciliary motion, and moved about with all the appearance of embryo-infusoria. Although the farther development of these bodies was not traced, the observations on this animal, and on another, the Urostyla grandis, afford sufficient proof that the infusoria may be propagated by minute separate germs, as well as by division of their bodies.

A similar production, but more numerous, of an internal progeny, has been observed in the microscopic parasitic animalcule termed Gregarina, which infests the intestinal canal of a number of insects, earth worms and some other invertebrate animals.*

The simple Gregarina consists of a single cell filled with granular substance, and containing a distinct nucleus. It has no intestinal canal, nor other internal organisation; is generally of an elongated shape, and creeps about by motions of slow contraction of its substance. The formation of the progeny or smaller bodies within the Gregarina is attended with a remarkable change in the parent animal, which has been carefully observed by Stein. This change, in which the animal appears double for a time, had been previously noticed by Kölliker and others, and had been interpreted by Kölliker as the conversion of a single animal into two, by a process analo-

Fig. 5.



Gregarinæ (from Kölliker.)

a, single; *b*, *c*, *d*, united; *e*, *f*, *g*, the formation of the navicella-like progeny; *h*, three of these navicellæ (from Stein).

* These animals were first accurately described by Leon Dufour in 1837 (Ann. des Sc. Nat. vol. vii. p. 10.). They have since been studied with great

gous to transverse fission. Stein, on the other hand, has been convinced by a very attentive observation of the different stages of this process, that it is of an opposite character, and that, previous to the development of the young progeny, two of the Gregarinæ have become fused, or united into one. As the two are about to unite, they gradually change their form from that of elongated planaria-like animalcules, to that nearly of hemispheres, closely pressed together; then a complete fusion or union occurs, and the whole of the granules of both having become amalgamated in one sphere, the development of the internal progeny takes place gradually from the mass. This progeny consists in a vast multitude of minute bodies, shaped like the Navicellæ (among the Diatomaceæ), but different from these bodies, and very probably constituting the reproductive germs or embryos of Gregarinæ. The development of this Navicella-like progeny into the Gregarina does not appear as yet to have been traced; as in this animal, like many other parasites, the progeny is required to migrate during its development from one stage to another, and the little bodies are passed out of the alimentary canal of the insect before undergoing farther changes.

The views and observations of Stein, however, should they be confirmed by others, would prove the very remarkable fact, that the phenomenon of conjugation, or fusion of two unicellular individuals, hitherto supposed to be confined to some of the simpler plants, as Closterium, Spirogyra and Zygnema, &c., may occur also in animals of a similar simple structure.

These observations on the Gregarina are not altogether of an isolated kind. In a recent interesting notice of this subject by V. Siebold *, he has called attention to the observation of Kölliker on the conjugation or fusion of two individuals of Actinophrys †, a spherical infusorian animalcule analogous to the Amœba or Rhizopoda, by its slowly contractile, amorphous texture, and its long, radiating, contractile processes. Kölliker observed two individuals of this animalcule to approach each other, adhere, and gradually to fuse into one, which soon assumed the same globular form, with the radiated contractile processes, as each of the two that formed it, and differing only from them by the increase of size which it sustained. This very curious observation has been confirmed by Stein, in an allied genus Podophyra, both of the sessile and pediculated kind; and V. Siebold has observed the same phenomenon in a species of Acineta belonging to the same family of Infusoria. Cohn, also, has repeated and confirmed Kölliker's observations in the Actinophrys sol, and has made a farther discovery of great interest in connection with the process of conjugation in these animals, having observed after the union, both in the Acineta and Actinophrys, the development, at certain periods, between the united individuals, of a spherical body of considerable size, vesicular form, and containing within it a nuclear formation of variable magnitude.

Although the farther development of this body has not yet been traced, it seems not improbable to V. Siebold that it may be analogous to the reproductive capsule or sporo-cyst of the conjugating Closterium or Zygnema*, from which bodies it seems to be certain that a number of reproductive spores are produced.

Since the foregoing was written, indeed, renewed researches by Stein † have come under my notice which are confirmatory of the view previously stated as to the reproductive process in Gregarina, and explain in a great degree the apparently incomplete observations of Pineau ‡ and others as to the varying conditions of Vorticella, and also extend our knowledge of the production of germs of the Infusoria. Stein observed the Vorticella microstoma to lose its pedicle, become free, assume the globular form, and at last to be enclosed in a cyst produced by exudation from its own body. After a time the band-like nucleus of the encysted Vorticella is divided into a number of small discoid bodies, not by a regular or progressive process of cell-cleavage, but at once and directly. These minute bodies gradually increase in size at the expense of the granular and fluid substance surrounding them in the cyst, and ultimately escape in the form exactly of Monas colpoda (of Ehrenberg). These very soon fix themselves; and a fine pedicle is developed at the place of attachment. In other instances the Vorticella-cyst was observed to send forth long contractile processes from its surface, and then assumed very much the form and appearance of an Acineta or Actinophrys; and in this case a new Vorticella was formed in the interior in the manner of a bud. The Vorticella, therefore, it would appear, is capable of reproduction in two modes,—by the development of embryoes from the divided nucleus, which Stein on this account proposes to call nucleus germinativus (the testis of Ehrenberg); and by gemmation from an intermediate Acineta form. The first form Stein would regard as the equivalent of sex-

success by various observers, as V. Siebold (Beitrag. Z. Naturgesch. Wirbellos. Thiere, 1839, p. 63.). Henle (Müller's Archiv, 1845, p. 369.), and Stein in the same, 1848, p. 182. Kölliker (Zeitsch. f. Wiss. Zool. 1848 and 1849), and as many as eighty different species of them have now been discovered.

* Zeitsch. f. Wissensch. Zool. March, 1851, p. 62.

† Op. cit. 1849, p. 207. In this very interesting memoir Kölliker has proved the animal nature of the Actinophrys by his observations on its contractility, and on the manner in which the particles of solid matters, vegetable and animal, are involved in its substance for the purpose of digestion, and their remains again rejected when that process is completed.

* See the Article Vegetable Ovum for an account of this process in the lower forms of plants.

† Zeitsch. fur Wissensch. Zool. Feb. 1852.

‡ Ann. des Scien. Nat. 1845 and 1848.

ual production ; the second as coming under the category of alternate generation ; and the Vorticella embryo of the Acineta-form either repeats its gemmal multiplication, or becomes encysted, and gives rise then by its nuclear division to embryonal production. Other new forms of Infusoria are described by Stein under the names Spirochona gemmipara, Dendrocometes paradoxus, and Lagenophrys vaginicola, ampulla, and nassa, in which the mode of reproduction is somewhat similar.

These observations at once show the importance of the views entertained by some authors as to the share the nucleus may take in new production, and strongly indicate that much still remains to be known from observation of the processes of reproduction among the Infusoria.

Should these observations be confirmed, another analogy, in addition to those already observed, will be shown to exist between the organisation and functions of the Protozoa, and those of the lowest plants.* The tendency of various other recent researches, to which it has been impossible to refer more particularly in this place, seems to be to show that, in addition to the more common and obvious mode of multiplication by division and gemmation, by which the Infusoria, when vigorous and well nourished, are reproduced, there are other means by which, in different circumstances, the more permanent reproduction of the species may be secured; that minute cells are formed within them for that purpose, which may at present be called reproductive cell-germs rather than ova, till a more complete knowledge shall have been obtained of their nature and of the circumstances attending their formation; and that it is very probable that in the protozoa, as in the simplest plants, the combination of the contents of two cells, to all appearance similar, may, as in the process of conjugation, be the necessary preliminary step to the development of the reproductive germs.

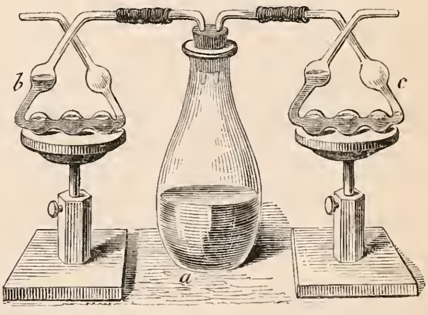
It ought at the same time to be kept in view that the Infusoria may, like many other animals, be subject, some to metamorphosis, and others to alternate generations. Already, since the publication of the great work of Ehrenberg, most important modifications of his system of these animals have been found necessary, and it seems almost certain that it is destined to undergo still farther changes, many of those forms which are now recognised as belonging to distinct genera and species being possibly no more than different stages of development of the same animal.

2nd. *Of the possibility of primary, direct, or non-parental production of animals, or of so-called spontaneous and equivocal generation.*

From what has before been stated as to the very general, and almost universal, existence of the sexual mode of generation among animals, and from the reasons that have been given for the belief that in those few and simple animals in which a sexual distinction has not yet been ascertained, there may still be propagation by means of minute germs, the reader will already have drawn a conclusion as to the very insufficient nature of the proof that can now be adduced in favour of the view that certain animals may arise independently of pre-existing individuals of the same species. The hypothesis might, perhaps, be at once dismissed with the remark of a recent writer*, "that it is safer to trust to generally prevailing laws, than to confide in such of our observations as are contrary to them." But as in the article GENERATION†, the author was led by a careful examination of the evidence then available on the subject, to admit the probability of the non-parental mode of production as an exceptional occurrence, at least among the lowest tribes of animals and plants, and as that hypothesis has since gradually lost more and more of its probability, from the accumulated opposing proofs resulting from more recent researches, so as, in his opinion, to be now no longer tenable, it may be proper at this place to review briefly the bearing of the present more advanced knowledge of the generative process upon this long and keenly debated question.

Admitting, in the meantime, that the ova, or separate germs of Infusoria, have not yet been discovered with certainty, there are not wanting direct experiments which demonstrate that in an infusion of organic matter which would, when exposed to the air, naturally furnish a rapid succession of these productions, the development of living organisms is entirely suspended, if the arrangements are made such as to render it impossible for any germ or other part of a previously existing infusorian animalcule or plant to be communicated to the infusion. The experiments of Schultze and of Schwann are valuable, as appearing to have secured, in a great measure, the above-mentioned conditions, without otherwise interfering with the validity of the result. The first of these ob-

Fig. 6.



Apparatus employed by Schultze to prevent the access of germs by the air to an infusion.

a, flask for infusion; *b*, tube, with caustic potash; *c*, tube, with sulphuric acid.

* See the recent work of Alex. Braun, entitled Die Verjungung in der Natur, Freiburg, 1849.

* Eschricht, in Edinr. New Phil. Journ. vol. xxxi. 1841. p. 355.

† P. 429.

servers* placed in a glass flask an infusion of organic matter, a portion of which was known from comparative trials, when left exposed to the open air, soon to have animalcules developed in it in great quantity, and he connected this vessel with a tubular apparatus, by two apertures, in such a manner that the air, which was made to pass frequently through the vessel containing the infusion, should be drawn through strong sulphuric acid, or potash solution, before reaching it; and Schwann † arranged a similar experiment, having in view to secure the like conditions, by causing the air, which had access to the infusion, to be previously passed through an iron tube at a red heat. Before the commencement of these experiments, the infusion and the apparatus were carefully subjected to the temperature of boiling-water, by which it was presumed the vitality of all ova, or germs, or other organic particles must have been destroyed: and the result was the same in both the series of experiments, — viz., that, after a considerable lapse of time, no animalcules nor confervoid plants were formed: but when the atmospheric air was afterwards allowed to pass freely over the same infusion, without being subjected to the processes before mentioned, a rapid production of infusory animalcules took place in the usual manner.

The results of these experiments appear to be on the whole satisfactory, and nearly to decide the question as far as relates to the probability of the introduction of the germs of Infusoria, &c., into infusions by the air. But, indeed, the failure of many experiments of this kind, when not performed with the most scrupulous accuracy, need not excite surprise, when the very indestructible nature of some kinds of infusory animalcules is considered. It has long been known, and has been ascertained by the careful experiments of Spallanzani, Bauer, and Doyère, that some of the Rotifera and Tardigrada are capable of supporting a high temperature without loss of life, and of being kept for years even in the state of complete dryness, without loss of vitality: and, although it must be admitted that these animals differ greatly in their organisation from the Polygastric Infusoria, and the latter appear to be very liable to destruction from slight causes, yet it is possible that their germs may resist destruction in a greater degree than their adult forms: and, should only one of these animalcules, or its germ, be left in any situation favourable to its development, it is easily understood, from what is known of the production of these beings, with what rapidity a vast multitude of them may be brought into existence by their ordinary process of fissiparous increase.

Most physiologists are inclined to reject as fanciful and inaccurate the alleged observations of the actual conversion of particles of organised or organic matter into living infusoria. At all events, statements of this kind are to be received with the greatest caution: such, for example, as the observations stated to have been made by Pineau*, who affirms that he has seen the direct conversion of particles of disintegrating muscular fibre, isinglass, and wheat-flour, into various forms of living infusoria.

The spermatic filaments also, which, so long as they were looked upon as independent animals, were referred to as examples of an undoubted spontaneous generation, furnish no evidence in favour of that hypothesis in the view in which they are now regarded by physiologists: for they are to be considered rather as a peculiar product of organic growth within the spermatic cells, somewhat analogous to the fine moving processes of the ciliated texture, than as distinct organisms.†

In so far, therefore, as the theory of spontaneous generation may have been supposed to derive support from the formation of the lower forms of plants and animals in infusions of organic matter, that hypothesis must be considered as having lost the greater share of its probability, if, indeed, it has not been entirely disproved: but it must at the same time be admitted that a more precise acquaintance with the nature of the germs from which these organisms take their origin is still required to render the arguments derived from this source entirely conclusive.‡

The external and internal parasites which infest the bodies of almost all animals have in former times been held to afford a still stronger presumption in favour of spontaneous generation than the production of infusoria; but it will be found that in this instance, to a much greater extent than in the other, the probability of the view has gradually passed away before the increasing knowledge which modern research has afforded of the various modes of propagation of these animals.

The ready communication of various Epizoa, or external parasites, from one animal to another is now well known, and accurate observations have demonstrated that in almost all instances this communication may be traced to the implantation of ova, or pregnant individuals into their parasitic abode, as in the researches on the Sarcoptes scabiei, &c.

The parasitic fungi, also, of various cutaneous diseases, as tinea, porrigo, plica polonica, foul ulcers, &c.; the yeast-plant, the vinegar-plant, and other minute fungi connected with fermentation; the contagious algæ of the batrachia and fishes; the muscardine of the silkworm, are all well proved to be communicable by the deposit of their spores, or some part of their substance, upon the external surfaces of the bodies of the animals on which they grow, or by their introduction into cavities opening on the exterior.

All the internal parasites, or Entozoa strictly

* Poggendorff's Annalen, 1837, and Edin. New Phil. Journ. vol. xxiii. p. 165.

† In paper on Fermentation, &c. in Poggendorff's Annalen, 1837, p. 184.

* Ann. d. Sc. Nat. March, 1845, p. 182.

† See Article Semen.

‡ Consult, especially, on the whole of this subject, Dujardin's Hist. Nat. des Infusoires, 1842.

so called, are now known to be capable of true sexual generation, by means of ova, in their perfect or complete condition, and the whole class is remarkable for the great development of the sexual organs, and the prodigious numbers of ova which they bring forth. But it has been ascertained that their ova are rarely developed into new beings in the place of the abode of the adult entozoa: they are commonly subject, therefore, to migration from one organ to another in the same individual, or from one animal to another, or from the parasitic to the free-living condition; and they have recently been discovered to present very remarkable changes of external form and internal organisation in their various habitations; so great, indeed, that many of them, previously believed to belong to species, and even to genera and families widely different, are now recognised as different conditions of the same animal or species, and that many forms, whose mode of generation was unknown, are found to be derived by indirect production from ova, in a manner which will be more particularly described under the next section.

Thus it appears that the only entozoa which are destitute of sexual organs, viz. those belonging to the division cystica, are very probably only imperfect forms of Taenia or other cestoids, which, so long as they are in the encysted or confined condition, do not reach their full development: but many of which, during their incomplete condition, are capable of being multiplied by a process analogous to gemmation.

The greater number of the entozoa breed only when in the alimentary canal of animals, and the ova are excreted along with the fœces: it is obvious, therefore, that very many ova must be destroyed, and that a few only are liable to gain those peculiar situations which are fitted to maintain them in their earlier conditions, or in their later stages, to bring them, as parasites, to their full state of development.

The entozoa are usually found, therefore, in their most advanced stage, in the alimentary canal. There seems, on the whole, little difficulty in accounting for the entrance of entozoa from without into the alimentary canal, or the pulmonary air-cells and other open cavities: and every new fact that has been observed relative to the occurrence of entozoa in man and animals, leads to the conclusion that the ova, or perhaps more frequently the earlier larval or undeveloped forms of the entozoa, gain access to these situations by introduction from without, and most frequently along with food and drink; in those instances at least in which the entozoa migrate from one animal to another, or from an animal to the free state before returning to the parasitic condition. But the entozoa, which are, in general, in an incomplete state when situated in the close cavities or solid textures of the organs of animals, sometimes make their way from these situations into the alimentary canal, there to undergo their final development. Such appears to be the case with the Strongylus armatus, living in an incomplete state in aneurismal sacs of the blood-vessels of the horse, and in a fully developed state in the intestine; the Strongylus vagans, in cysts of the porpoise, and afterwards free in the lungs; the Ligula or Bothriocephalus solidus, in cysts of the abdominal cavity of fishes, and afterwards in their perfect state in the alimentary canal of sea-birds. The Trichina and Echinorrhynchi, imbedded in the muscular flesh in great quantities, are no doubt imperfect forms of other worms, which must migrate from these situations to attain to their complete state.

With regard to the manner in which the entozoa inhabiting the close cavities of the body, or imbedded in the solid substance of organs, either in the free or encysted condition, gain access to these situations, which has to many appeared inexplicable, excepting on the hypothesis of their arising actually in the places which they inhabit, observations are no less decided in proving them to be of external introduction.

In the first place it may be stated that, although the ova of a considerable number of the entozoa are of so considerable a size as to render it improbable that they have passed as such through the capillary vessels, yet few, if any, of these larger kinds are observed encysted, and in others the ova are extremely minute, and might, without difficulty, be carried through most of the capillary vessels.

In the next place it may be mentioned that the embryoes, or earlier forms of various parasites, and the ova of others, have been observed in considerable numbers in the circulating blood of various animals *, as showing that by this means the entozoa may be carried in their small and early condition into any part of the body of an animal which is fitted to afford the conditions favourable to their farther development.

But in what manner have these bodies gained an entrance into the blood-vessels, or, in other instances, how may entozoa have penetrated into cavities or the parenchyma of organs, without being conveyed through the blood-vessels? To this question, also, recent observations seem to furnish a satisfactory answer: for it has been ascertained that, in a number of instances, smaller or larger entozoa, but especially the former, pierce the tissues of animals with great apparent facility, being frequently provided in the young state with an apparatus of sharp hooks for that special purpose. Some of them have been observed in the act of passing through the

* I may here refer to the original observations of Schmitz, (Berlin, 1826), and the more recent ones of Valentin Gruby, Gluge, Vogt, and others. See Valentin, Repertorium for 1842 and 1843. The Annual Report in Müller's Archiv. for the same years, and in Wiegmann's Archiv. for Naturgesch. Valentin's account of the Ova of Distoma in the fluid covering the medulla oblongata of a fœtal sheep (Müller's Archiv. 1840, p. 317), and V. Siebold's Article 'Parasites' in R. Wagner's Handwörterbuch der Physiologie.

solid substance of organs or through membranes; and from the various stages of advancement of others already referred to, seen in different parts of the same animal, little doubt can prevail that they must have done the same: but the aperture through which they make their way, besides being in most instances very minute, seems to close very rapidly and completely after them. So that the occurrence of entozoa in entirely isolated cavities — such as the aqueous chamber of the eye, or in the parenchyma of solid organs, — does not now present to our minds any valid objection to the view that in all instances they are introduced from without; and it will be apparent, from the same considerations, that even the occurrence of entozoa in the fœtus, of which there are undoubted instances, and to which great importance has been attached as an argument in favour of their spontaneous origin, may be explained on the supposition of their ova, or young, passing from the maternal parent, through the blood-vessels of the umbilical cord, as is known to happen with various poisons.

The whole history, then, of this remarkable class of animals, as it is now known, tends to support the general conclusion that they are all capable in their complete state of sexual reproduction, and that they gain the various sites of their parasitic habitations by introduction of their ova, or embryoes, or of more advanced stages of their growth from without, either directly into the open cavities, or more indirectly, by piercing the coats of vessels, membranes, &c., into the close cavities and the parenchyma of solid organs.*

A candid review of the whole evidence on this question leads to the inevitable conclusion, that, though all the difficulties or doubts which surround it are by no means completely removed, the hypothesis of primary or spontaneous generation receives little or no direct support from the accurate observation of the mode of origin of those animals which alone were supposed to afford proofs of such a kind of production; and that this view must, therefore, on the strongest grounds of analogy, be in the meantime abandoned, for that which attributes the origin and reproduction of all organised beings to an undeviating connection through ova or germs, seeds or spores, between new individuals and others of identical species which have previously existed. And if the present somewhat imperfect state of knowledge does not permit us to affirm this absolutely, as the result of direct observation, the exceptions are so few and unimportant, that they may be disregarded in the overwhelming evidence of a positive character in favour of the opinion, derived from analogy, that every organic being, if not produced in actual union with another, derives its origin from a germ or some such connecting part that has proceeded from a being of the same kind.

If this be the present state of the argument in respect to the hypothesis of the first origin of organic beings, it need scarcely be added that the opinion which has attributed the production of various animals to conversion or gradual transmutation out of other species or genera, has still less of real to be adduced in its support. In the long series of ages in which authentic observations have been made on animals, no such examples have been ascertained, and there are no established facts which give any substantial grounds for believing that in the natural or wild state of animals there is any departure from that undeviating succession of specific resemblance between parent and offspring, which seems to form one of the most constant of the laws of organic nature with which we are acquainted.

3rd. *Production of dissimilar individuals among sexual animals by a non-sexual process: so-called Alternate Generations.*

From the foregoing general views it appears that in all Vertebrated Animals, and in by far the greater number of Invertebrated animals, the process of permanent reproduction consists in the development of the new being from the blastodermic mass formed by a peculiar process of cytogenesis in the fecundated ovum. But, as has already been shortly stated, there are some varieties among them in regard to the degree of directness with which the product of development from the ovum arrives at that state of maturity, or sexual completeness, in which it is capable of renewing the act of sexual generation. These varieties may be classed as follows:—1st. The product of the ovum, being single, attains by a gradual process of development, when it leaves the ovum at birth, to nearly the same form and structure as its parents: this is generally called *Embryological Development*. 2nd. The product of the ovum, being single, is born or leaves the egg at an early period, and while comparatively imperfect, or, as it is called, in a *larva* state, and by one or more successive changes of development of a marked kind, afterwards reaches the specific or typical form: these changes are usually called *Metamorphoses*. 3rd. The product of development from the ovum does not itself become a complete animal, but gives rise, by a peculiar mode of generation of a non-sexual character, and therefore different from that by which fecundated ova are formed, to a new body, or to successive progenies of new bodies, one or more of which ultimately attains to the specific resemblance of the sexual parents by which

* As to the bearing of a knowledge of the habits &c. of the Entozoa upon the question of their spontaneous origin, consult the able essay by Eschricht; "Inquiries concerning the Origin of Intestinal Worms &c." in Edin. New Phil. Journ. vol. xxxi. p. 314. 1841, the article on Parasites by V. Siebold, in R. Wagner's Handwört. der Physiol.; E. Blanchard's Researches on the Structure &c. of Intestinal Worms, in Ann. d. Sc. Nat. 1848 and 1849, particularly vol. vii. p. 121. Dujardin's systematic work, Hist. Nat. des Helminthes, 1845. And in connection with this and the whole subject of spontaneous generation, the Systematic Treatises on Physiology of Burdach, J. Müller, Valentin, and Longet.

the ova were produced. This is the "Alternating Generation" of Steenstrup, or what we might with Mr. Owen, in contrast to Metamorphosis, call a process of *Metagenesis**; and of which the single and multiple varieties might be distinguished according as the intermediate progeny consists of one or of successive new productions.

In the two first and best known forms of sexual generation, the term Development has been usually given to a gradual process of changing and advancing growth by which the new animal is formed out of the ovum, till the period when it leaves it, or is said to be born; and the term Metamorphosis has been generally applied to certain more marked and sudden changes of growth, apparently depending on the circumstance of the embryo or young animal having left the ovum, or having been born, at an early period in a comparatively incomplete state of growth. But in establishing such a distinction between these terms, it is not meant to be affirmed that the changes which a young animal subject to metamorphosis undergoes are individually or on the whole greater than those which occur in an animal which attains to its full growth by a process of development; but merely that the one series of changes is less gradual than the other; and that the more marked changes which accompany metamorphoses are related to certain conditions necessary to enable the animal which is born at an early period immediately to perform those acts which belong to its independent existence. It would indeed not be difficult to show that the changes which a mammal or a bird undergoes during its viviparous or oviparous development, are quite as remarkable and complete as those which occur in the change of a Batrachian reptile from its aquatic to that of its air-breathing condition, or of an insect from its larva to its complete form.

In both of these instances one individual only is developed from the ovum, and that individual itself at last reaches sexual completeness, and as being well understood they need not be longer dwelt upon here. But in the varieties of the reproductive process which are now to be more particularly noticed, the individual that proceeds directly from the ovum does not itself pass through the whole series of changes which are necessary to bring it to the form of the fully developed animal; but before it possesses any sexual organs, or has attained to sexual maturity, it produces from a minute germ formed in its body by a non-sexual process, a new individual, or a succession of individuals, the last of which only attains to the specific resemblance of the parents, and acquiring sexual organs propagates the species by means of ova. This is the modification of the reproductive process already termed *Metagenesis*, and which has received so much attention under the name of "Alternate Generations" since the publication of Steenstrup's celebrated treatise under the title of "Generations-Wechsel" in 1842.*

No examples of this peculiar modification of the reproductive process have been known to occur in the Vertebrata, and with one exception they are confined to the lower and simpler of the classes of Invertebrated animals. They are not, however, entirely confined to the very lowest classes of these animals as distinguished by the Zoologist, but rather to the simpler and less developed members of each of the several classes in which instances of them have been hitherto observed.

The essential nature of this form of reproduction consists, then, in the development from the ovum of an individual which is dissimilar from the parent or parents producing the ovum, and in the succeeding production from that individual, by a non-sexual process, of a progeny of one or more, or a succession of individuals, of which the last of the series resumes the parental form. While in animals, therefore, reproduced by the ordinary form of generation, the species is composed of entirely similar individuals, or of individuals differing only in sex; in those animals which are subject to the alternate or intermediate generation, the species includes a variety of individuals usually of dissimilar form; of which some are without sex, and others are complete as regards the development of sexual organs.

It has appeared to some authors that the phenomena in question are to be regarded as no more than peculiar modifications of the processes of development or metamorphosis, of such a nature that the product of the ovum becomes multiple instead of, as is more usual, remaining in its single individuality. But to admit the correctness of this view, it would be necessary to employ these terms in a sense widely different from that commonly given to them; and, indeed, to modify the ideas of these processes of embryological development in a greater degree than seems warranted by what is at present known of their nature.

The name of *larva* is usually given to the imperfectly developed animal that is born or leaves the egg at a comparatively early period, and fitted for independent existence in that state; and in the changes of metamorphosis by which that larva attains to the complete specific form, great as these changes may in some instances be, we recognise that it is the individual produced from the ovum which itself undergoes these changes; whereas in the various kinds of alternate generation, it is always by the formation of an entirely new individual, arising from a minute germ connected with the first, but to be distinguished from its parts, and without a sexual process, that the species is at last completed. The new individual may be single or there may be a multitude of them; they may remain connected with the one producing them or they

* Adopting a term which has been used by Mr. Owen in his Lectures. Med. Times, vol. xx. 1849.

* A work which appeared originally in the Danish language, and in German in 1842, and of which an excellent translation into English has been published by the Ray Society in 1845.

may be detached and live independently, but they nevertheless constitute different animals, and cannot be regarded in any other light than as so many individuals distinct from the one producing them, although all are descended from one ovum, or all are necessary to make up the entire species.

And it is further to be observed that each of these several animals may be subject to individual metamorphosis, and that in some classes there is so gradual a transition from individual change to new production that it may be difficult to determine to which of these forms of reproductive development their phenomena ought to be referred.

In that part of the article which treats specially of development our attention may again be called to some of the more remarkable examples of individual metamorphosis that are known: at present it is intended rather to bring prominently forward those instances of alternate generation which have been discovered since the publication of the Article GENERATION, or which, if previously known. may now be viewed in a different light, in consequence of being brought into comparison with other observations of a similar kind and of more recent discovery.

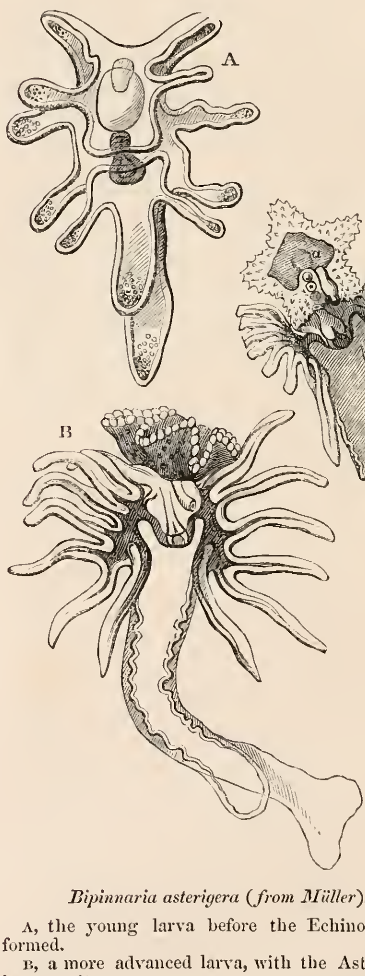
We may first consider some examples of this process, or of one very analogous to it, in which the new animal is single.

Echinodermata.— In several orders of this class a variety of the reproductive process has of late years been pointed out, in regard to which it may be doubted whether it is most of the nature of a metamorphosis or a metagenesis, but which, as it has been considered by J. Müller, the discoverer of the most interesting and remarkable of its phenomena, as in some measure analogous to the alternating generation, I will mention in this place; the more so, that it might almost be looked upon as forming the connecting link between the direct and the alternating processes of reproduction.

In some of the Echinodermata it appears from the earlier observations of Sars that the young produced from the ova are developed directly into the parental form, passing however through several marked modifications in the early stages of development. Thus, some of the star-fishes (*Asteracanthion glacialis*, Sars) leave the egg as a ciliated free moving animalcule, then they become pediculated and attach themselves, have four club-shaped processes developed on them, and, lastly, they pass by the development of the rays and the internal organs into the complete form; but here the whole, or nearly the whole, germinal mass of the ovum is converted into the embryo or larva, and the whole, or nearly the whole, of this undergoes the farther changes of conversion into the complete and sexual animal.*

From the researches of J. Müller it appears that the mode of development now described is exceptional among the Echinodermata, and that in other families of the order Asteriadæ, and in the Ophiura and Echinidæ, an embryo or larva of a peculiar kind, is formed by direct development from the fecundated ovum, which is not itself converted into the complete animal, but rather serves as a temporary stock from which the perfect animal is subsequently formed in a manner that may be compared to gemmation. But it does not appear that more than one individual is developed from each primary larva stock, and this gradually dies away, so soon as its attached offspring has made some advance in its formation. This body, described under the name of Bipinnaria asterigera, as connected with an Asterias, is a comparatively large animal, with a long pediculated body, twelve or fourteen tentacles, an alimentary canal, consisting of mouth, gullet, stomach, in

Fig. 7.



Bipinnaria asterigera (*from Müller*).

A, the young larva before the Echinoderm is formed.

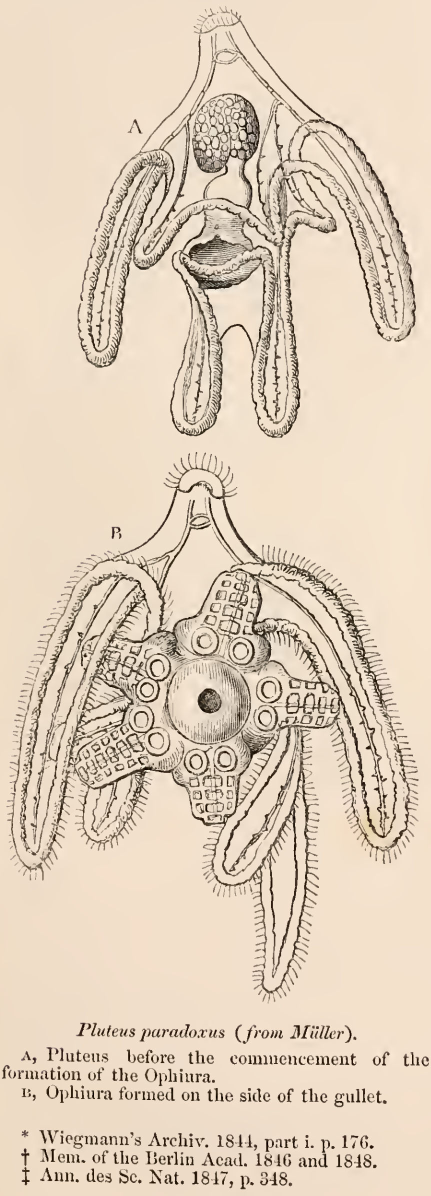
B, a more advanced larva, with the Asterias on its summit.

C, the Asterias torn up to show its stomach, a continuation of the alimentary canal of the larva.

* Sars, Fauna Littor. Norvegiæ, 1846; and Ann. des Sciences Nat.; Agassiz, Lectures on Comparative Embryology, New York, 1849; and a Letter from Desor to J. Müller, in Archiv. für Physiol. 1849, p. 79.

testine, and anus, and moves actively through the water. Sars who had observed this body in 1835, was the first to suggest in 1844 that it might be the early condition of a star-fish *, and this view was confirmed by the admirable researches of J. Müller †, and by observations of Koren and Danielson ‡, who have shown that the Asterias is gradually formed out of a small granular mass which surrounds the stomach of the Bipinnaria, and becomes separated from the stock when in a comparatively early state of advancement. The larva stock moves about afterwards for a few days,

Fig. 8.



Pluteus paradoxus (*from Müller*).

A, Pluteus before the commencement of the formation of the Ophiura.

B, Ophiura formed on the side of the gullet.

* Wiegmann's Archiv. 1844, part i. p. 176.
† Mem. of the Berlin Acad. 1846 and 1848.
‡ Ann. des Sc. Nat. 1847, p. 348.

and then appears to die without giving rise to any farther progeny.

The gemmiparous larva of some other kinds of the Echinodermata was first described by J. Müller as a distinct animal, under the name of Pluteus, before he was acquainted with the phenomena of its subsequent development: in 1846 he traced the relation between one kind of this body which he had called Pluteus paradoxus, and the Ophiura, and between another kind of Pluteus and Echinus, ascertaining it to be the same that has just been stated to exist between the Bipinnaria and the Asterias. The Pluteus presents the form of a quadrangular pyramidal frame, with four large ciliated limbs at the angles, and four smaller ones suspended from the middle below, while the upper part is surmounted by a sort of dome. It bears some resemblance to a Beroë, and might be described as the ciliograde larva of an Echinoderm. The form differs, however, somewhat for various species of Ophiura and Echinus.

In the centre of the dome and round the mouth of the Pluteus a granular mass is described, and from the side of this, non-symmetrically, the gemmation of the new individual proceeds. The Pluteus moves at first with great activity through the water, propelled by its ciliated limbs and cirrhi; but as the new Ophiura or Echinus buds from it and spreads more and more over its dome, the Pluteus shrinks, becomes less active, and at last disappears.*

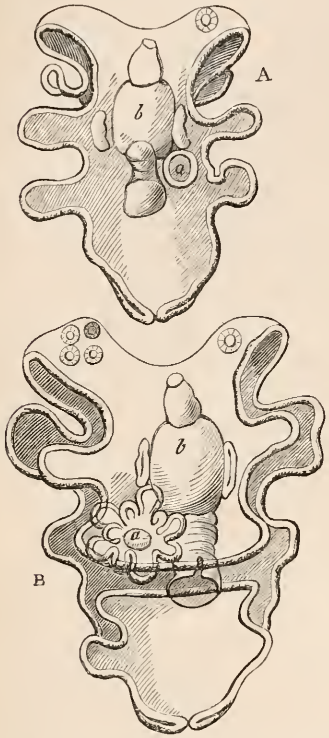
Various other forms of the Pluteus-like animal have been described by Müller, and the process of gemmation has been traced by which the new Echinoderm takes its rise within them. The result of these discoveries is already to throw an entirely new light on the nature and organisation of this class of animals; but the species of all of those observed is not yet determined, and something still remains to be learned of the exact mode of origin of the new animal. By some † the process has been looked upon merely as a secondary development from the remains of the yolk attached to the parts first formed; but the researches of Müller do not appear to give support to such a view; and would rather appear to show (as in Auricularia, *fig.* 9.), that the new animal is formed from a minute germ in a determinate part of the parent animal without that germ being traced to the yolk of the egg.

In a farther series of researches on the larvæ and metamorphoses of the Echinodermata ‡, J. Müller has pointed out that the Holothuridæ are formed from a larva body somewhat analogous to the Pluteus, but that, instead of a process of new formation, the whole of the larva is converted by a very remarkable metamorphosis into the Holothuria; and he has been enabled, from his

* J. Müller, in Mem. of Berlin Acad. 1846 and 1848; Derbes, in Ann. des Sc. Nat. 1847.
† As Carpenter, loc. cit. p. 939.
‡ Memoirs of the Acad. of Scien. of Berlin, Nov. 1849, and April 1850, published in 1851, p. 35.

own researches and the comparison of some others, to bring the whole of the Echinodermata under a general view, the result of which is the determination of the three following varieties of metamorphoses and production among them. In all of them the embryo, immediately developed from the ovum, has a bilateral symmetrical form, and passes by the subsequent metamorphosis into the radiated type. This change is, however, more or less direct, or by intermediate forms.

Fig. 9.



Auricularia, or larva of Echinoderm (*from Müller*).

A, young larva of Auricularia. *b*, alimentary canal; *a*, Echinoderm beginning to be formed.

B, larger larva of the same kind, *a* Echinoderm farther advanced.

1. In the first variety the change of the bilateral larva, or embryo, into an Echinoderm takes place at its earliest period, when the embryo has a general covering of cilia, but not the special ciliated borders or limbs of the Pluteus. A part of the body of the embryo takes the form of the Echinoderm; the rest of it is absorbed into the body of the new animal. This occurs in a part of the Asteriadæ, as in Echinaster, Asteracanthion, and others, described by Sars, Agassiz, Desor, and Müller.

2. In the second variety the change occurs when the larva is fully organised, that is, when it possesses digestive organs and a special motor apparatus of ciliated borders or limbs. The Echinoderm is placed upon the Pluteus somewhat in the manner of a picture on an easel, or a piece of embroidery in its frame and stand, and incorporates a part of the digestive cavity with itself. The remains of the larva gradually disappear, as in Ophiura and Echinus; or are broken off and die, as in Bipinnaria.

3. In the third variety the change of the larva takes place twice. First, it passes from the bilateral type with ciliated borders into the radiate type, and having taken something of the shape of a barrel, it acquires a larval locomotive apparatus consisting of ciliated hoops; and then from this state the Echinoderm is developed without any part of the larva being separated. Either the Echinoderm is formed of a part of the Vermiform larva, and the rest of the larva is absorbed into the Echinoderm, as in Tornaria; or the whole larva is simultaneously transformed into the Echinoderm, as in Holothuria.

From Busch's observations it appears that the Comatula passes very rapidly through the stage of the bilateral form into that which Müller has called pupa with ciliated crowns. It is also an interesting fact in connection with the history of animal metamorphoses, that the early condition of the Comatula is that of a pedunculated Crinoid.

Müller has remarked that these phenomena partake in part of the nature of metamorphosis, and in part of that of the non-sexual gemmation of the alternate generations. As the Echinoderm arises like a bud in the larva, there is alternate generation; but as the essential internal organs (that is, the alimentary canal from the stomach to the anus, but not the mouth and gullet) are taken into the new animal, there is also true metamorphosis. "I understand," says he, "by alternate generations nothing more than the succession of two forms of organism, of which the one arises in or upon the other as a minimum, or as a bud; the second, that is, the developed bud, is destined for sexual generation, producing from its ova the non-sexual larva, which again is destined for gemmation."*

Adopting the view that the Echinodermata present an example of alternate generation, it is to be observed that the product is single in all the instances known: but in all the other forms of intermediate or alternate generation hereafter to be noticed, the product of non-sexual gemmation is multiple.

Polypina. — The animals usually comprehended in the general denomination of Polypes or Polypina present very various kinds of structure and degrees of complication in their organisation; and recent researches, as to their mode of development, which point out that some of them are subject to a process of alternate or dissimilar generation, would appear to indicate a very different distribution

* Loc. cit. p. 106. The researches of J. Müller on this subject have been published in a separate form, as well as in the Mem. of the Berlin Acad. These Memoirs, and others on the same subject, will be found also in Müller's Archiv. 1846, p. 108; 1847, p. 160; 1848, p. 113; 1849, pp. 79. 84. 364. 400; and 1850, p. 452.

of these animals in the zoological system than that which has hitherto been followed. Most Naturalists are now disposed to separate from the true Polypina the Bryozoa, or so-called Ciliobrachiate Polypes, which, though presenting a considerable resemblance to the Polypes in their external anthoid appearance, yet approach much more nearly to the Tunicated Acephalous Mollusca by their internal organisation; and remarkable affinities have been pointed out between some of the Polypina and Acalephæ, which show that these classes, though very dissimilar in their external forms and mode of life, are in reality very closely allied in structure.

The greater number of the Polypina are aggregate or compound animals, that is, consist naturally of groups of individuals united or associated together on a common stem and branches, or on a more solid stock. But the common fresh water Polype, or Hydra, and the various Actiniæ of the sea coast, are, to a certain extent, exceptions to this general rule, and, as we shall see, differ also in regard to their mode of reproduction from most of the other families of this division of animals. The Actinia is usually a single animal: no doubt it is multiplied occasionally by buds, but these are thrown off and become developed usually in an isolated position. The Hydra sometimes occurs as a single animal, but more frequently during summer, and when well nourished, as a compound one; the multiple individuals being developed by gemmation from the first or principal stock, and also themselves forming younger progenies by budding; but the individuals so formed on the Hydra generally

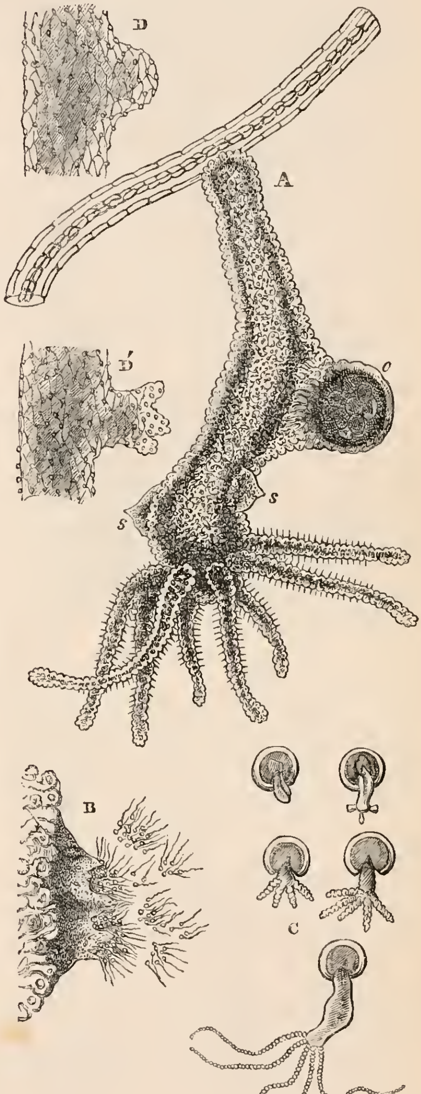
Fig. 10.

Hydra viridis in different stages of extension and contraction, reproducing gemmiparously, attached to the roots of duck-weed. (*From Roesel.*)

separate from the parent stock when they have attained to maturity, migrate, and establish themselves as independent animals, to form new buds.

Both of these animals are capable of propagation by ova formed in the sexual way: in Actinia this seems to be the more common mode of its multiplication, the ova being fecundated and developed within the body of the hermaphrodite parent; but in Hydra it would appear that it is principally in the autumn, on the approach of cold weather, that the sexual mode of propagation is substituted

Fig. 11.



Hydra viridis.

A, Hydra of autumn, bearing an ovum, *o*, and two spermatic capsules, *s*, *s*. B, spermatic capsule burst artificially, showing spermatozoa.

C (from Laurent), ova with young Hydra in various stages of development hanging out of them.

D, D′ (from Laurent), portions of the body of summer Hydra, with a bud sprouting. D, the earliest; D′, more advanced, showing the texture to be the same as the rest of the body.

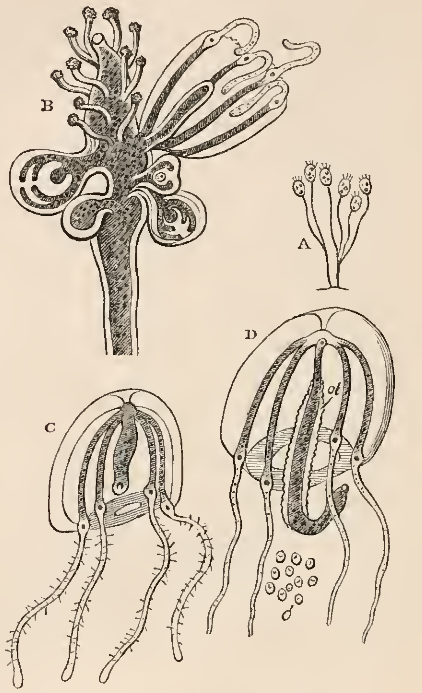
for that of gemmation which takes place throughout the whole of the summer.*

The ova of Hydra are simple vesicular capsules of a brownish colour formed in the substance of the wall of the animal's body, and separated from it previous to the development of the young; while the spermatic filaments are formed in smaller conical capsules placed nearer to the base of the tentacula either in the same or in different individuals.† The formation of the young Polype has been observed by Laurent ‡ to take place directly from the internal substance of the ovum, in which, however, he has not traced in a sufficiently complete manner the individual steps of the changes of development (*see fig.* 11. c.). The origin of the ovum in this animal is shown to be quite different from that of a bud: the former having the shape of a distinct vesicle from an early period, the latter not being perceptibly more than an extension of some part of the substance of the wall of the body, and precisely of the same colour and structure (*see fig.* 11. D, D′.).

The Hydra, therefore, while propagating very frequently by gemmation, is capable of reproduction also by fecundated ova, which are directly developed into the parental form. But many of the true Compound Polypes present examples, in their multiplication by gemmation, of the production of intermediate forms of animals between the ova and the perfect sexual individual, — a mode of reproduction, therefore, which may be referred to Steenstrup's general law of Alternate Generations.

Thus, to begin with the simplest form of these animals bearing the nearest resemblance to the Hydra, in the Coryne and Syncoryne, at certain seasons of the year, multiplication takes place from the stem or root by gemmation, the buds being developed in the form of attached Polypes; but at other times there are developed from the buds, without the concurrence of sexual organs, a set of delicate Medusa-like animals, similar to the Oceania, or those of the naked-eyed kind: these soon become detached, swim about freely in the water, acquire some of them male and others female sexual organs, and produce fecundated ova. These ova give rise, by their development, to a ciliated moving embryo: this soon becomes fixed to a spot, and is gradually converted into a Polype, similar to that from which the Medusa-like animals were formed.*

Fig. 12.



Syncoryne, developing a Medusoid progeny. Oceania (From Désor.)

A, natural size.

B, a portion enlarged, showing the budding of Medusoids in different stages.

C, one of the Medusoids, naturally detached.

D, another, farther advanced; *o t*, ovary, or testicle, placed on the alimentary canal; *o′*, ova.

R. Wagner appears to have been the first to observe Medusoid bodies produced from the Polype animals, as in Coryne aculeata, in 1833†, but the more full observation of the remarkable phenomenon of their formation is due to the researches of Sars, Löwen, Steenstrup, and Van Beneden, who have ascertained the relations of the Polype larva and Medusoid progeny, and the production of ova from the latter. Dujardin‡ has also carefully traced the production of the free Medusoid bodies from a Syncoryne, which he has called Stauridia, and has farther ascertained the sexual condition of these Medusoids, observed the formation of their ova, and the subsequent development of these ova into Polypes.

* This effect of the cold season in changing the mode of production from gemmation to oviparous formation, thus checking growth, but providing for the preservation of the species through the winter, is, as remarked by Dr. Carpenter, an interesting analogy with the change that is known to occur in the mode of production of the Aphis insect; see Principles of Physiology.

† The co-existence of ovigerous and spermigerous capsules on the body of the Hydra has been observed by many, as, first by B. de Jussieu, in 1743; (Abhand. der Swed. Acad. 1746, vol. viii. p. 211): by Trembley, in 1744 (Mém. sur les Polypes d'Eau douce); by Rösel (Insecten-Belustigung); Pallas, in 1776 (Karakteristik der Thier-pflanzen, p. 53); and more recently by Ehrenberg, in 1836 and 1838 (Verhand. der Naturforsch. Freunde in Berlin, 1838, p. 14); V. Siebold (Lehrbuch der Vergleich. Anat.); and by myself (Edin. New Phil. Journ. 1847).

‡ Nouv. Rech. sur les Hydres d'Eau douce, 1844, Voyage de la Bonite.

* See fig. of Syncoryna Sarsii, from Sars, Fauna Litt. Norveg. 1846; and Steenstrup's figures of Coryne fritillaria, tab. 1. figs. 41. 43, and Desor, in Ann. des Sc. Nat. 1840, pl. 2. figs. 13. to 16.

† Isis for 1833, p. 256. Also in Coryne vulgaris, in Icones Zootom. Tab. xxi. 1841.

‡ Annal. des Sc. Nat. 1845.

In a certain number of the Campanulariæ, Sertulariæ, and Tubulariæ, of which the internal structure is more complex than in the Coryne, and in which the Polype always naturally presents a branched form, or groups of distinct Polype heads formed upon a common stem by gemmation, it is now well ascertained that the Polype state is not the only nor the complete condition of the animal, but that by

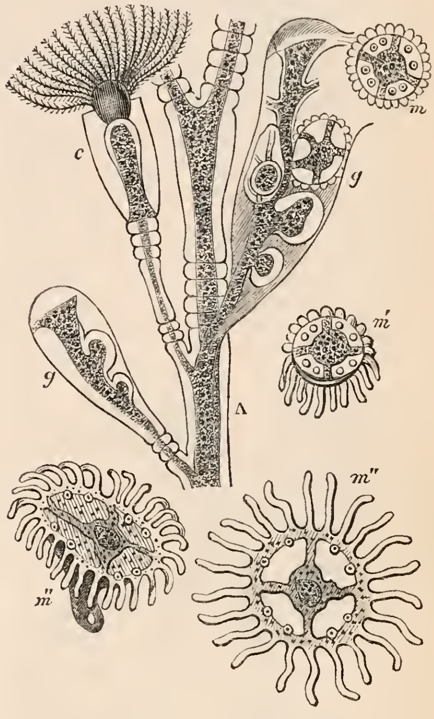
Fig. 13.

Branch of Sertularia geniculata, magnified, shewing polypes, and ovigerous capsules.

a process, in some instances similar to that above described, in others, somewhat different from it, a set of bodies, charged with the office of the sexual production of the ova, are developed in place of the more ordinary Polype heads or individuals. In the Campanularia gelatinosa, according to Van Beneden, the generative heads are close bell-shaped capsules, within which small Medusoid bodies are developed by a process apparently analogous to gemmation, or, at all events, without sexual generation, and each of these Medusoids becoming free, move about in the adjacent fluid as independent animals. The farther destination or changes of these Medusoid bodies have not yet been observed, but from parallel observations in other similar animals, it is believed that they afterwards attain to sexual completeness, and form ova which are developed into the Polype form.*

But the interesting observations of Lovèn*, and also some previous observations of Lister †, would show that in the Campanularia

Fig. 14.



Campanularia. (*From Désor.*)

A, portion of a branched stem, magnified. *c*, non-sexual head or individual; *g g*, two capsules, or modified heads, producing Medusoids by gemmation, in different stages; *m*, Medusoid escaping; *m' m''*, Medusoids more advanced, moving freely by the contractions of their disc.

geniculata, and in Tubularia, the Medusa-like bodies may in some instances not be detached from the Polype heads or capsules, and may even not be developed fully into the Medusa form, but nevertheless produce their ova in that attached situation, and thus give rise to ciliated embryoes, which, when excluded, move for a time, and then, like the others arising from the detached Medusæ, become converted into Polypes.

According to Désor, of Boston ‡, the same Campanularia may at one time produce two kinds of capsules, the one set containing ova the other spermatozoa; the Medusoid progeny not being developed, and the ova giving rise to forms similar to the parent Polype: and M. S. Schultze, of Greifswald, has confirmed this statement§, apparently without the know-

* See the View of Campanularia geniculata, by Van Beneden, in Mém. de l'Acad. de Bruxelles, 1844, vol. xvii.; and Ann. des Sc. Nat. tom. xx. p. 350, 1843. See also the very interesting account of Tubularia, in Dalyell's Remarkable Animals of Scotland.

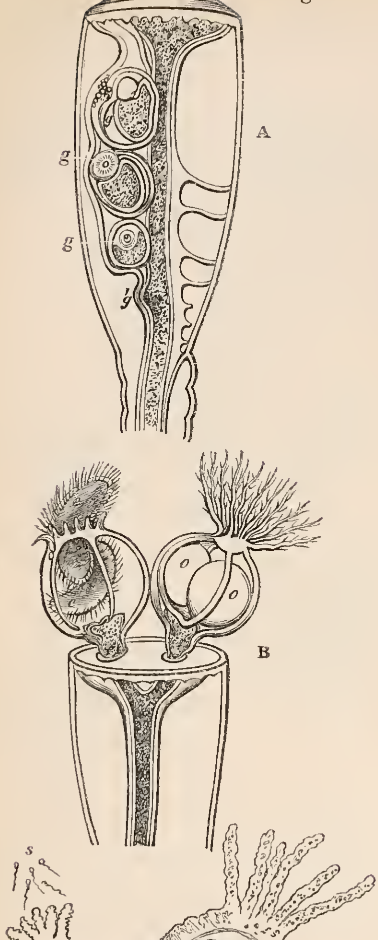
* In Wiegmann's Archiv, 1837.

† Phil. Trans. 1834.

‡ Ann. des Sc. Nat. 1849, xii. p. 208.

§ Müller's Archiv, 1850, p. 53.

Fig. 15.



Campanularia geniculata (A and B *from Lovèn, as copied by Steenstrup*).

A, modified or bell-shaped polype head or capsule, producing the female individuals at *g,g,g*; the earliest of these budding from the granular stem *g'*.

B, the female heads expanded from the bell: one of them containing two ova, *o o*; the other containing two ciliated embryoes, of which one is issuing at the summit of the attached medusoid, *e e*.

C (*from Schultze*), male heads of the same species of Campanularia; *p*, upper part of the polype head, or bell-shaped capsule; *c*, sexual capsule, or modified attached Medusoid, containing spermatozoa; *c'*, another of the same, burst, and spermatozoa discharged, *s*; *c''*, other spermatic capsules advancing behind the first.

ledge of Désor's observations, and has farther proved the necessity of fecundation for the development of the ova so produced in the Campanularia geniculata (*see fig.* 15. C.).

The various modes of production as they have been observed in the Tubularia by Van Beneden*, have been so fully detailed in the Article POLYPIFERA, that the reader is referred to that article for an account of them. But it is to be observed that the reconversion of the Medusoid progeny of this animal into the Polype form described by that author (see Article POLYPIFERA, *fig.* 50., p. 45.), has not received confirmation from the researches of other naturalists.

Much remains still to be learned of this remarkable process; but enough has been ascertained to show that in a certain number of animals, usually known as passing the greater part of their lives in the Compound Polype condition, the state of sexual completeness frequently belongs not to the Polype, but to a progeny having the form of a Medusa, and produced by a non-sexual process of development from the Polype stem.

Acalephæ. — Some time before the peculiar history of the development of the Polypina, now sketched, was discovered, an equally curious and unexpected phasis in the generation of some Acalephæ or Medusæ had been established by the concurrent researches of several inquirers; by which it was shown that the animals familiarly known as sea nettles existed for a time in the early stages of their development in the form of an attached polypoid, and were produced by a process analogous to gemmation, or transverse fission, in numbers from this Polype stock.†

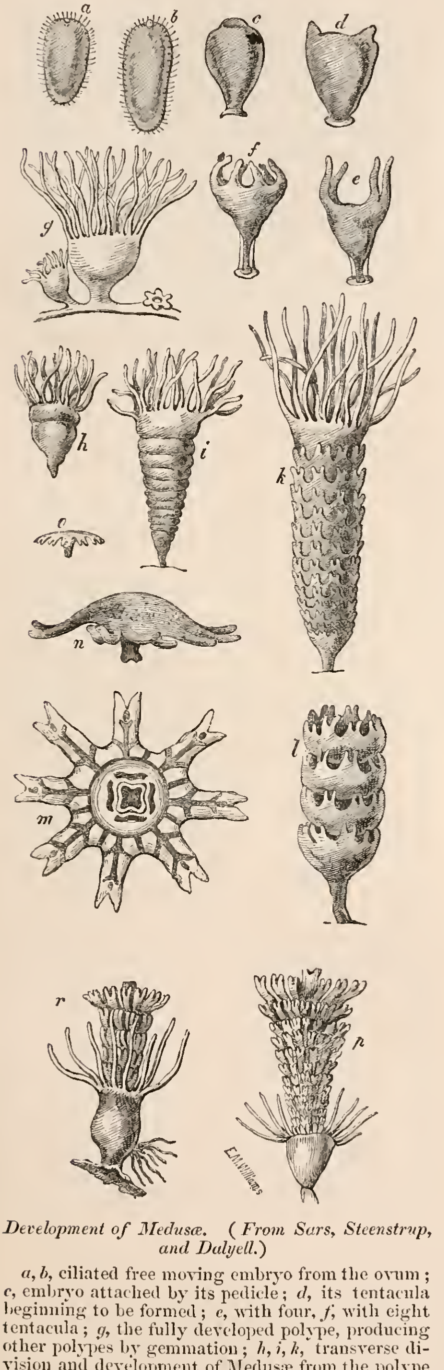
Adult Medusæ are perfect animals in which the male and female sexual organs are placed on distinct individuals. The fecundated ova which they produce are first developed into a ciliated moving animalcule somewhat like a polygastric infusorian. This creature, after

* Mém. de l'Acad. de Bruxelles, tom. xvii.

† The Swedish naturalist Sars appears to have taken the lead in this discovery, as early as 1828, by his observation of the Compound Polypoid, from which the Medusæ are thrown off; and subsequently, in 1835, by the discovery that this animal, or strobila, is really the young condition of a Medusa, or rather a colony of Medusæ. Very interesting observations of a similar kind were published by Dalzell on this body, under the name of Hydra tuba, in 1836, but his observations probably date from an earlier period (Edin. New Phil. Journ. vol. xxi. 1836). Sars pursued the investigation of the process further, and published the results in Wiegmann's Archiv, 1837; but the complete account of his observations was not published in the same Journal till 1841; see also Ann. des Sc. Nat. for 1841. In the meantime V. Siebold had arrived at precisely similar conclusions, and subsequently their views have been fully confirmed by Dalyell (Remarkable Animals of Scotland); J. Reid (Ann. of Nat. Hist. 1848, and Physiolog. Researches); Steenstrup (Alternations of Generation); and Huxley (Phil. Trans. 1849, part ii.) See also Dujardin, Mém. sur le Développement des Méduses et des Polypes Hydraires, Ann. des Sc. Nat. 1845. The reader is also referred to Dana's great work on Zoophytes in the United States Exploring Expedition. Philad. 1848.

undergoing a slight change of form, fixes itself by the narrowest end, and acquires tentacles like a Polype at the other, amounting for some time to eight. In this condition it appears to

Fig. 16.



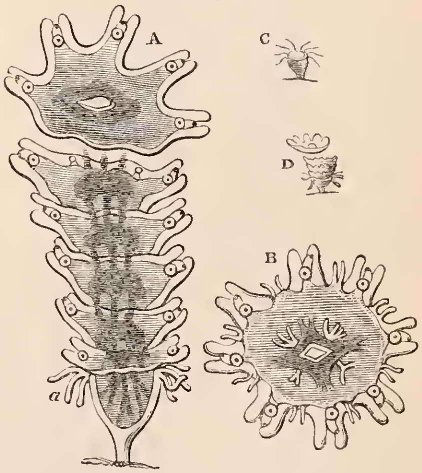
Development of Medusæ. (*From Sars, Steenstrup, and Dalyell.*)

a, b, ciliated free moving embryo from the ovum; *c,* embryo attached by its pedicle; *d,* its tentacula beginning to be formed; *e,* with four, *f,* with eight tentacula; *g,* the fully developed polype, producing other polypes by gemmation; *h, i, k,* transverse division and development of Medusæ from the polype stock or strobila; *l,* a pile consisting of four Medusoids just about to separate; *m, n,* and lower lateral view of Medusæ separated from the polype stock; *o,* more advanced, natural size: *p, r,* (*from Dalyell*), *p,* a pile of medusa discs separating, and new tentacula formed on the polype at the base; *r,* the same, with more of the discs separated; the strobila returning to its polype state and budding at the side.

be capable of multiplying itself, or producing other similar attached Polypes by gemmation from its side or base, or from a running stolon below it. The subsequent change of each of these polypoids is remarkable. It has been described by Sars and Dalyell as follows: — The body undergoing some elongation becomes partially divided by transverse grooves, into a range or column of imperfect Medusæ, attached still to each other by their adjacent surfaces, but presenting at their borders, in various degrees of advancement, the division into rays or lobes which belong to the Medusa; the upper or terminal one having developed upon it a set of radiated processes distinct from the tentacles of the Polype and much longer than those of the rest. These young Medusæ are successively separated from the stock by the deepening of the transverse clefts between them. They then move about as independent animals, and proceed in their farther growth and development to sexual and other completeness. These bodies, therefore, are subject to two kinds of multiplication, which are very different: by simple gemmation a number or a colony of Strobilæ may be produced, and by transverse fission and development a number of Medusæ may be thrown off from each Strobila.

A considerable number of the Medusa progeny having been separated, the Strobila stock generally returns to its polypoid condition,

Fig. 17.



Production of Medusæ (*Aurelia aurita*) *from Polype stock.* (*From Désor.*)

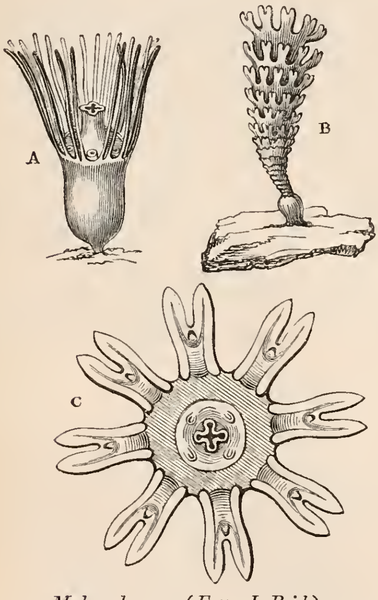
A, Medusa-form larvæ on the stock above the polype, which remains at the base, *a.*

B, lower surface of a detached Medusa.

C, D, natural size. Young Medusæ forming from the polype above its disc.

and may remain for a long time in that state; continuing to multiply by budding into others of the same kind, and occasionally giving rise by the process of fission to its Medusa progeny. The observations of J. Reid * have shown that the Polype or polypoid stock may remain for a very long time in this condition without forming any Medusa progeny; and these observations, as well as those of Steenstrup and of Désor, appear to show that these Polypes bear a considerable resemblance in their internal structure to the Medusæ which they produce by gemmation. The latter author, indeed, is inclined to believe that the new Medusa animals are produced not by a mere transverse fission of the Polype, but by successive gemmation on its summit, that is, round its mouth and within the tentacula; and he states that he has observed the Polype remaining with its tentacles at the base of the Strobila of Medusæ. The observations of Dalzell and

Fig. 18.



Medusa larva. (*From J. Reid.*)

A, Polype before it has undergone any gemmation of Medusæ, showing the mouth and four canal openings.

B, the strobila or larva forming Medusæ.

C, lower surface of one of the young Medusæ, after separation.

J. Reid appear, however, inconsistent with this view; but it is possible that there may be varieties in respect to the mode of formation of the Medusa progeny, so that in one set the tentacles of the Polype may be included in the upper Medusa, and when all the progeny is separated, new tentacles may be formed on the Polype stock at the base, while in others the budding Medusa may be within the circle of the tentacula of the Polype.

It appears from recent investigations that others of the Acalephæ also undergo remarkable processes of non-sexual multiplication. According to Huxley's recent most interesting researches *, the Physsophoridæ, Diphydæ, and Physalia, are to be regarded as compound organisms in which the floating processes of most various form are analogous to Polype or attached Medusa individuals, which are the bearers of sexual organs, in some of one kind, in others of both, and others of which are neuter, on the same compound stock.† These are probably a progeny developed by budding from a single individual, which is the parent stem.

By these discoveries a remarkable relation is shown to exist between the medusoid and polypoid animals. Some we have been accustomed to see principally in their largest and most developed condition as Medusæ, others are best known in that polypoid condition in which they remain for the longest time; but we must regard that condition in which sexual reproduction takes place as the complete one, and this we have seen is in both the Acaleph or Medusa form, while the Polype or polypoid state, however permanent it may appear, is to be looked upon as a preparatory stage, in which, it is true, multiplication of its own kind may occur by gemmation, but which can only effect the true reproduction of the species by forming its progene of Medusans to which is committed the offic of producing the fecundated ova. This, therefore, is another example of multiple metagenesis, or alternating generation.‡

Mollusca. — Among the Mollusca the only examples of alternate generation that are yet known have been observed in the Tunicated Acephala: and among these, three modifications of the reproductive process are known in the Bryozoa, Ascidia, and Salpidæ.

The Bryozoa, or so-called Ciliobrachiate Polypes, long ranked with the Polypes on account of their union in branched groups, their radiated arms, and retractile body, but now regarded as more nearly allied by their internal organisation to the Tunicated Mollusca, present a very marked example of the multiplication by budding of the progeny of a single ovum. These animals never continue for any considerable time as single or distinct individuals, but, multiplying by gemmation, form numerous colonies, in which the new individuals remain connected with the primitive one from which they have proceeded and with each other. They thus always constitute compound groups spreading from the first individual as from a centre. All the individuals of the group may acquire sexual completeness, and the male and female organs are united in each individual: the ova are fecundated within the cavity of the mantle;

* Ann. and Mag. of Nat. Hist. 1848.

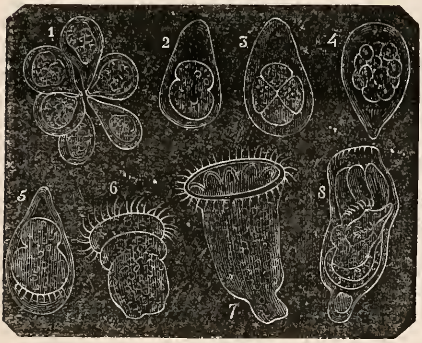
* Phil. Trans. 1849, Pt. ii.

† Professor Goodsir has informed me that his observations on Stephanomaia are quite confirmatory of this view.

‡ See also on this subject the interesting treatise by Prof. E. Forbes, on the Naked-eyed Medusæ, in Ray Soc. Pub. 1848.

on leaving the parent body they become developed into a ciliated embryo, which, for a time, moves freely about, then becomes fixed, undergoes farther changes in being developed,

Fig. 19.



A series illustrating the development by ova of Pedicellaria. (*After Van Beneden.*)

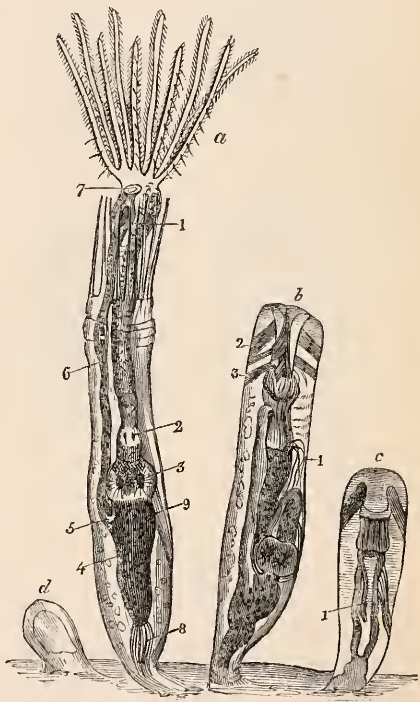
and now from its own body in some, and in others only from the spreading part of the stem or base which supports it, proceeds the gemmation of other individuals of the colony, all of which apparently are capable of sexual generation when they arrive at maturity.‡

The Ascidian Tunicata present another modification of the reproductive process now under consideration. Two forms of these animals exist, both perfect, viz. the simple and the compound; but these are not related to each other in the same manner as the two kinds of Salpians; for each kind is capable of propagating its like by generation. The solitary ones rarely multiply by gemmation, and when they do so the individuals separate from the stock; but the compound animals always undergo this mode of multiplication, and the multitude of individual Ascidians are in this form collected together in a mass of various shape, in which the circulation of fluids is for a time common among the different individuals. The individual animals produced from the stock by gemmation attain to sexual completeness, and propagate by means of ova, in the same manner as the solitary or distinct Ascidiæ do.

The young of these animals undergo a remarkable metamorphosis: they are first excluded from the egg in the form of a moving tailed body, somewhat like a minute tadpole; and this caudal organ of motion is lost previous to their becoming fixed, and the development of the more complex organisation.†

Although the changes to which both the Bryozoa and Ascidian Tunicata are subject in their early state present some very striking phenomena of metamorphosis, yet there is nothing in either which fully deserves the name of alternate generation, for all the individuals of which these compound animal structures consist are alike sexually perfect, and there does not appear to subsist any necessary connection between the nonsexual process of multiplication, and the subsequent exercise of the sexual function. There are, in fact, scarcely any intermediate stages of non-sexual existence such as are described in the true instances of alternate generation. It is deserving of notice, however, that Löwig and Kölliker are of opinion that in some of the Botryllidæ numerous embryoes are at once developed from a single ovum by its division, these individuals subsequently multiplying by gemmation into the perfect sexual animals.

Fig. 20.



Bowerbankia densa. (*After Farre.*)

a, one of the animals fully expanded.
b, a similar animal completely retracted.
c, an immature animal.
d, one of the gemmæ in its earliest state.

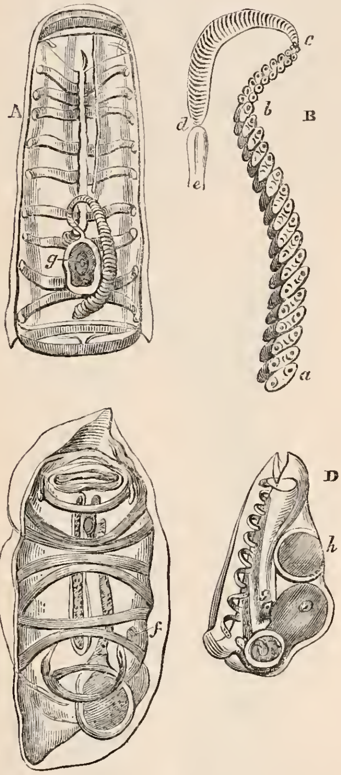
Salpidæ. — The most marked example of alternating generation among the Tunicata is that which, since its first discovery by Chamisso, in 1819, has been known to occur in the Salpidæ. This process has been so well and fully described in the article TUNICATA, that it is not necessary to give more than a short outline of it in this place. These animals are known in two states, viz. solitary and ag-

* Van Beneden, in Mém. de Bruxelles, tom. xviii. See the Article Polypifera, for an account of these researches.

† See Mr. Rupert Jones's excellent Article TUNICATA for an account of these phenomena, and the special Memoirs of Milne-Edwards, sur les Ascidies Composées, &c., Paris, 1832; Löwig and Kölliker, in Ann. des Sc. Nat. April, 1846; Van Beneden, sur les Ascidies Simples, Brussels, 1847.

gregated; the latter being not organically united like the compound polypes, but merely adhering more or less strongly to one another so as to form a chain. The aggregated, but not the solitary kind, possess sexual organs; and it would appear, though this is not yet determined with certainty, that all the individuals of one chain are of a similar sex either male or female.

Fig. 21.



Solitary and aggregated Salpæ. (*From Sars.*)

A, solitary Salpa, with chain of aggregated ones, *g*, budding from it.

B, this chain magnified, shewing the successive sets in different stages.

C, one of the more advanced aggregated Salpæ from a chain, *f*, the place of a fœtus formed by sexual generation.

D, fœtus from another more advanced, magnified; *h*, the yolk, by which it adhered to the parent; *g*, the place of the germ for the aggregated chain.

All the individuals of a chain of aggregated Salpæ are produced from a solitary one by a process of internal gemmation, or gradual development from an internal stolon, or germ-stock, from which they are detached gradually and in successive groups: all the individuals of the chain are contained within a tube, and become united to each other after their development, presenting a series of groups of different degrees of advancement; but the individuals in each group being nearly at the same stage of development.

The distinct or single Salpæ, which, with the exception of the want of the sexual organs, do not differ materially from the individuals of the aggregated chain, are produced from fecundated ova which are developed within the body of the parent. These ova differ from the germs from which the aggregated individuals take their origin in the possession of a yolk, and external envelope. Their development proceeds to its termination within the parent body, and the young Salpa is already provided with the internal stolon for the gemmation of its chain progeny, before it passes into its separate state of existence.

The solitary Salpæ may be looked upon, therefore, probably as incomplete or larva forms, and the aggregated are the fully developed sexual individuals. The generation of this animal, therefore, is precisely an example of that succession of two different kinds of individuals which has been distinguished as alternation of generations; each fecundated ovum of the sexual individuals being developed into an animal which never acquires sexual organs, and which produces by a process apparently of the nature of gemmation, a numerous brood of individuals associated in a chain; all of which are sexually perfect, one set developing only spermatozoa, and the females among them being the producers of the ova, which are the source of the new generation.*

Although no other instances of alternate generation have yet been observed in the class of Mollusca, yet it is possible that modifications of this process may hereafter be discovered. An observation related by Agassiz†, in regard to the development of the ovum in one of the Eolidæ, deserves to be recorded, as it may be found to constitute an approach to the metagenetic process. After having described the usual process of division of the yolk in which the first stages of development consist, and the farther progress of formation in the Eolis, he says, — "But the most curious phenomenon which takes place is this; that the whole yolk does not constantly go to form one single individual. But there may be instances when the mass of yolk, which has been subdivided into cells, is itself divided into two or three or more masses, which grow independently, several individual animals arising from one mass of yolk, which thus divides."

Entozoa.—Among the Entozoa the process of reproduction is effected by very various means. All the Nematoidea, or round worms, are of distinct sexes; and their fecundated ova are developed into the parental form without any metamorphosis of a marked kind, (excepting perhaps in the Echinorrhynchi, the

* See Savigny, Mém. sur les Anim. sans Vertèb. 1816; Chamisso, De Salpis, 1819; Meyen, Ueber die Salpen; Eschricht, in the Isis, 1842; Sars, Fauna Littor. Norvegiae, 1846; Krohn, Ann. des Scien. Nat. July, 1846; who first pointed out the existence of spermatozoa in certain individuals of the aggregated chain.

† Lect. on Comparative Embryology, Boston, 1849, p. 81.

process of generation in which is not fully understood,) nor any intermediate process of gemmation. A few of them, however, appear to become encysted in the parenchyma of organs in their young or undeveloped condition, and some in a form different from the parent, as in the Trichina of the muscles, the so called Filaria of the peritoneal cavity of fishes, and the Vibrio tritici. These encysted Nematoidea have not been observed to be possessed of sexual organs *, and they are not known to be multiplied by gemmation; it is probable, therefore that, to attain the place of their full development, they must be subject to migrations from one animal to another, either directly or in other ways, as through water and vegetables. The ova of these animals appear to possess a remarkable tenacity of life, as exhibited by their long and obstinate resistance to the noxious effects of external agents. †

The Cystic, Cestoid, and Trematode orders of the Entozoa present a more varied process of generation, the investigation of which has of late years attracted considerable attention, and which has led to most interesting results as to the nature and relations of several forms of these animals, which were previously regarded as of a most anomalous kind. The Cestoid and Trematode Entozoa have long been known to possess the sexual organs in the hermaphrodite arrangement, and to produce fecundated ova; while the Cystic Entozoa have been observed to multiply only without sexual organs, and by a process analogous to gemmation, and their first origin has been till lately involved in the deepest obscurity. We shall presently see that many, if not the whole of them, may be either undeveloped or metamorphosed aberrant forms of cestoid or trematode animals. ‡

This view appears first to have been suggested by Steenstrup, in connection with his researches on alternate generations §; and it has since been adopted, in somewhat different forms, by V. Siebold, Blanchard, Dujardin, and Van Beneden, and rendered extremely probable by the researches of these and some other observers. Previous to the adoption of this view, helminthologists, looking upon the Cystic Entozoa as distinct and independent animals, were at a loss whether to regard them as ascertained exceptions to the sexual mode of propagation, or to continue to prosecute their inquiries in the hope of being able to discover a process of generation in them analogous to that prevailing in the greater majority of the animal kingdom; and many were thus misled into the error of searching for ova where none existed or were required. Thus Gulliver erroneously described certain calcareous particles in the membrane of Cysticercus as the ova of the animal*, and H. D. Goodsir, in his instructive paper on the production of the young in that animal, and in the other forms of Cystic Entozoa †, failed to distinguish between that which might be merely a process of gemmation and the origin of the embryoes from true ova.‡

Cystic Entozoa. — The Cystic Entozoa present themselves in three principal forms, viz. Acephalocyst, Cænurus, and Cysticercus. The two first are usually found as compound or aggregated animals; the last is more frequently seen in the single or isolated condition.

Some of the vesicular hydatid tumours, constituting the various kinds of so called acephalocysts, have long been known to contain small Echinococci floating in the fluid of their interior. Repeated observations have demonstrated the existence of these animals in the acephalocysts; and it seems very probable that, in the end, it will be necessary to withdraw the distinctions between the various kinds of these cysts, as they will all, by sufficiently accurate observation, be found, at some period of their growth, to contain in a more or less complete condition, the small animals of Echinococci, or their remains. §

The Echinococci are produced by nonsexual generation, or by gemmation from the membrane of the vesicle, probably from the middle or germinal membrane, as it has been

* See a Memoir by V. Siebold, on the Nonsexual Nematoidea, in Wiegmann's Archiv, 1838.

† Dr. Henry Nelson and I have observed the development of the ova in Ascaris mystax to proceed for several days, while the parent bodies containing them were immersed in oil of turpentine.

‡ For a notice of the generation of the minute parasitic animalcule called Gregarina, see the previous account of the reproduction of Infusoria.

§ See Ray Society's Translation, 1845, p. 100. "It is not unlikely," says Steenstrup, "that in course of time, it may happen with them (Cystic Entozoa), as it has with the whole division of the asexual Trematoda of Siebold, viz. Cercaria, &c., that they must be rejected from the system as being earlier forms of development, or earlier generations of other animals." V. Siebold remarks in a note at p. 157, of his Lehrbuch der Vergleich. Anat. part i. published in 1845, "Here the doubt arises whether the asexual Cystica really deserve to be considered as independent animals. It is very probable that the vesicular worms are undeveloped Cestoids," &c. See also note at p. 111. Von Siebold has developed these views more fully in a recent Mem. in the Zeitsch. für Wissensch. Zool. July, 1850, translated in the Ann. des Scien. Nat. vol. xv. 1851, p. 177; and in the article Parasites, in Wagner's Handwörterbuch der Physiologie. E. Blanchard in his Rech. sur l'Organis. des Vers, in Ann. des Scien. Nat. 1847 vol. vii. p. 120. excludes entirely the Cystica from a separate place in the systematic arrangement, bringing them under Cestoidea, and affirms decidedly that the distinction between them ought now to cease, as they are shown to be different states of the same animals. He refers to De Blainville as having previously entertained the same view. See also Dujardin, in Annal. des Scien. Nat. for 1843, and Hist. Nat. des Helminthes, 1845; Miescher, Bericht üb. die Verhand. der Naturforsch. Gesellsch. in Basel, 1840; and Van Beneden, Ann. des Scien. Nat. 1851, p. 309; and a work on the Entozoa, published at Brussels, in 1850, which I have not seen.

* Med. Chir. Trans. of Lond. vol. xxiv. 1841.

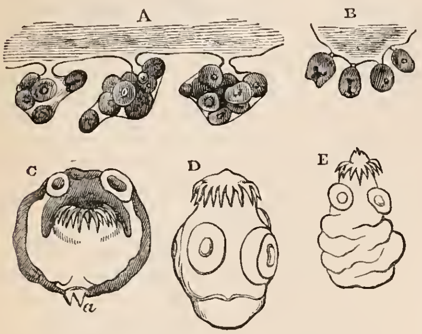
† Trans. Roy. Soc. Edin. vol. xv. 1844, and in Anat. and Path. Observations, 1845.

‡ See also Rose, in Med. Chir. Trans. vol. xxxi. 1848.

§ See V. Siebold's Report on Zoology, in Ray Society's publications, for 1845 and 1847; also Burdach's Physiol. B. ii.

called by H. D. Goodsir; and they have been observed, in some instances, attached in pediculated vesicles, singly or in groups, to the inner

Fig. 22.



Echinococcus hominis. (*From Wilson.*)

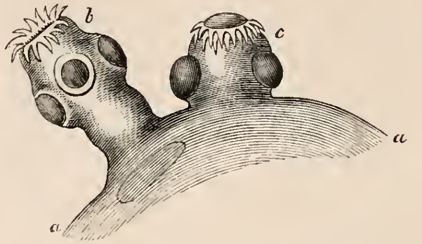
A and B, grouped and single Echinococci, attached by peduncles to the inner membrane of the cyst. C, a contracted, and D, an expanded Echinococcus; *a*, the peduncle. E, a more advanced animal, shrivelled.

surface of the cyst.* While enclosed in the pediculated vesicles, the head of each echinococcus is retracted within the short vesicular body in a manner which seems to be general among the young of encysted Entozoa. They are afterwards set free, and in this state are found floating as minute whitish particles in the fluid of the cyst. They then present the appearance of minute heads of Tæniæ, with a short body scarcely larger than the head; the latter part being furnished with a terminal double circle of hooklets, and four suckers.†

The mode of gemmation may probably vary in different circumstances, more particularly in regard to the extent to which the progeny of gemmation may or may not repeat the formation of others of the same kind; but every thing that is known of the acephalocystic productions seems to point to the view that they are all nearly allied, and that they are abnormal or aberrant conditions of Tænia-larvæ, which, when they become encysted, are incapable of development into the cestoid form which belongs to those that have reached the free intestinal habitation.

The Cænurus, which has been met with principally in the brain and some other parts of the sheep and some other Ruminating animals, consists of a large cyst or vesicle with a number of small heads projecting on its external surface: each head resembles closely that of an echinococcus animalcule, presenting the same circle of hooklets and four suckers. According to H. D. Goodsir, they are attached to the middle membrane of the cyst, from which they sprout at first, carrying the outer one along with them: the neck contains cells, from which it is supposed other young animals or heads may be formed.*

Fig. 23.

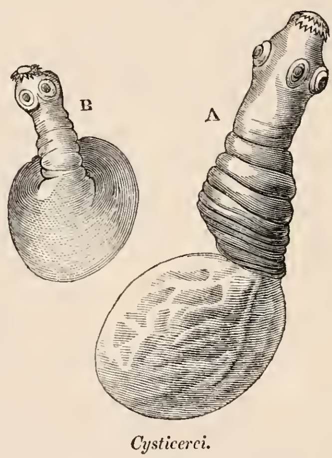


Cænurus cerebralis, magnified. (*After Bremser.*)

a a, part of the general vesicle; *b*, an expanded head; *c*, a shorter head, showing the double circle of hooklets.

The Cysticercus has been described in two forms; 1st, in its simply vesicular state, and 2nd, in its fasciolated condition, or in its transition, as it may be held, to the cestoid, or tape form. The vesicular Cysticercus has

Fig. 24.



Cysticerci.

A, Cysticercus longicollis (from Bremser), enlarged. B, Cysticercus from the human eye (extracted by Dr. Mackenzie), magnified five diameters.

only one head; but the structure of that part is precisely the same as in the Cænurus and Echinococcus, and, we may add, not far different from that of the Tænia itself. They are usually developed singly, that is each vesicle with one head: but some observers† allege that they have seen internal vesicles near the neck, which they look upon as young, or as a progeny of gemmation in that situation.

The Cysticercus fasciolaris, as it has been observed in the rat and mouse, presents the remarkable fact of a Tænia in various states of development, from the vesicular condition of

* E. Wilson's paper in Med. Chir. Trans. xxviii. 1845; and H. D. Goodsir, Anat. and Path. Obs.

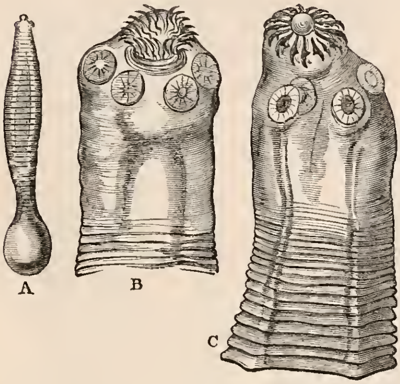
† See Curling, in Med. Chir. Trans. vol. xxiii.; and Müller, in Jahrsbericht of Archiv, 1836. p. 106.

* H. D. Goodsir, loc. cit.

† As Rose and H. D. Goodsir, loc. cit.

the true Cysticercus, to a form in which the caudal vesicle has diminished to such an extent as almost to have disappeared, while at the same time the body has been divided into segments by transverse grooves, as in the Tænia; and in some instances these segments have even acquired sexual organs while the animal was still encysted, a circumstance which has never been observed in any true Cysticercus.

Fig. 25.



Cysticercus fasciolaris of the Mouse, and Tænia crassicollis of the Cat.

A, Cysticercus fasciolaris from the liver of the mouse, natural size. B, the head of the same, magnified. (From Dujardin.)

C, head and first segments of the body of Tænia crassicollis of the cat, showing the double circle of hooks; a few of the smaller under circle being seen where one or two of the larger ones have fallen off.

A close comparison of the structure of the Cysticercus fasciolaris of the rat and mouse in its various stages of development with the Tænia crassicollis of the domestic cat, has shown an almost complete similarity between these animals, and has suggested the view that the encysted Tænia (which the Cysticercus fasciolaris in truth is) may attain its full development as a Tænia in the intestinal canal of those animals which prey upon the smaller Rodentia, in whose liver it begins to be developed in its first simple vesicular form, and gives the greatest probability to the supposition that there may be a similar general relation between the Cystic and Cestoid Entozoa, not of the same animals, but between the tapeworms of different tribes of predaceous animals and the vesicular worms of others serving them as food.*

The different phases of development, therefore, in which the so-called Cysticercus fasciolaris has been seen in the same and in different animals which they inhabit, leave little doubt that they are encysted Tæniæ, which proceed to a much more advanced stage of development than is usual with the vesicular and encysted form of these Entozoa; and we are warranted, from the great similarity of structure, in adopting the view that the true vesicular Cysticerci, the Cænuri and Echinococci, are morbid or metamorphosed and aberrant conditions of the embryoes of various Tæniæ, which may be capable, to a greater or less degree, in different kinds of animals, of multiplying their own incomplete forms by a process of non-sexual gemmation, but which never, in the encysted condition (except in the instances already referred to of the fasciolated kind), attain to sexual completeness; but which either undergo a retrograde change, and thus form tumours and various pathological deposits in the seat of their cysts, or become developed to such an extent as to be injurious or destructive to the animal in which they reside.*

Free Tapeworms.—Three principal forms of cestoid worms are now distinguished from one another, viz. Tæniæ, Bothriocephali, and Tetrarhynchi; the two first have long been known and sufficiently well characterised in their fully grown condition, though little understood in their early or incomplete states; the history of the third, until recently, has been involved in great obscurity, as it has been most variously described by different observers both in the earlier and more advanced stages of its growth. It appears now to be ascertained that all of these cestoids are complete animals, with a single head, a body composed of a multitude of segments, each of which contains male and female sexual organs, which are developed only when the entozoon is living free in the alimentary canal of animals belonging principally to the Vertebrata. The Tæniæ inhabit chiefly the alimentary canal of mammals and birds; the Bothriocephali and Tetrarhynchi more frequently that of fishes and reptiles, and the latter a few mollusca. The Tetrarhynchi have been more frequently described in the encysted and imperfect condition than in the full-grown form, and in such varieties, that V. Siebold has mentioned about sixty different kinds of worms described by various authors under distinct appellations, which might, according to him, be

* Dujardin, Hist. Nat. des Helminthes, 1845. E. Blanchard (who does not appear to have fully appreciated the necessity of change of habitation for the entire development of the tænia), Sur l'Organisation des Vers, Ann. des Scien. Nat. 1848, tom. x. p. 348. V. Siebold, in Zeitsch. f. Wiss. Zool. 1850, and Ann. des Sciences Nat. 1851. I am indebted to Dr. Henry Nelson, for an account of some interesting researches on this subject which formed a part of his Inaugural Dissertation "On the Development of the Entozoa," on obtaining the degree of M. D. at the University of Edinburgh, in 1850. The limits of this article prevent me from entering into the details of Dr. Nelson's observations, which have not yet been published. It is enough to mention that a very careful comparison of the Cysticercus fasciolaris of the mouse and rat, in various stages of its development, with the Tænia crassicollis of the cat, enabled him to confirm, in a most satisfactory manner, the view which, unknown to Dr. Nelson, had previously been taken by V. Siebold, that these cystic and cestoid forms are different stages of one and the same animal. See also *Leuckart* on Cysticerci, in Wiegmann's and Erichson's Archiv for 1848.

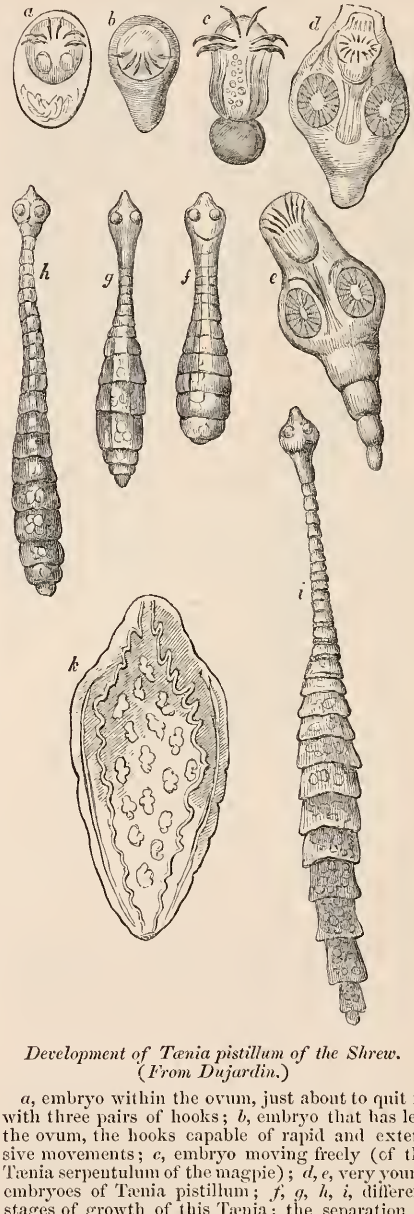
* See Gulliver, in Med. Chir. Trans. 1841.

brought under the genus Tetrarhynchus. In fact, this kind of animal undergoes such remarkable changes in its transition from its first simple Echinococcus-like encysted form to its free segmented sexual Tænia-like shape, that it is not wonderful that its history should have been obscure, and that great doubts should still prevail with some Helminthologists as to its origin, development, and zoological relations.*

It has already been observed, that none of these three kinds of Cestoid Entozoa attain to sexual completeness while they are encysted ; and it seems probable that they are all subject, more or less, to migration, in order to gain their free habitation in the alimentary canal of animals, where their segments acquire the male and female generative organs. The fecundated ova, produced in enormous numbers from each segment, do not in general, so far as is known, become developed into embryoes in the intestine of the animal inhabited by the Cestoid, but are evacuated along with the fæces, either separately after being discharged from the oviducts of the Cestoid, or before their discharge by the disjunction of the more ripe terminal segments from the rest of the animal. The migrations to which the ova and young of the Tænioid animals are thus made subject have hitherto opposed so great an obstacle to the observation of their development, that we are as yet in possession of very few continued series of observations in which the whole progress of development from the ovum to the complete segmented animal has been traced. Some important contributions of this kind have, however, recently been made, and the great modifications which the views of comparative embryologists have undergone, from the novel and various aspects in which many of the phenomena of development are to be regarded in instances of alternate generations, have already indicated paths of inquiry by which this very curious and intricate history may ere long be completely unravelled. The accompanying figures from Dujardin's work show the progress of formation of a small Tænia inhabiting the Shrew, and give a sufficiently good idea of the nature of this process in a Tænia, which consists of comparatively few segments (*fig.* 96. *a* to *i*.).

Von Siebold has traced with care a part of the process of development of a minute Cestoid inhabiting the pulmonary sac of the red snail (*Arion empiricorum*) in the encysted condition. Into this situation the minute Tæniæ are introduced from the exterior : they consist of the head with its double circlet of ten hooks each, and four suckers, and a body which is at first entirely destitute of segments, not longer than the head, and forming a soft vesicle, within which (as in other Cystic Entozoa previously mentioned) the head is retracted, so as to give the whole a globular shape. V. Siebold regards it as nearly certain that these minute Tæniæ only attain to their segmented and complete sexual condition when they have been located in the alimentary canal of Vertebrata (Birds and others) preying upon the snails in which the younger forms of the Tæniæ reside.

Fig. 26.



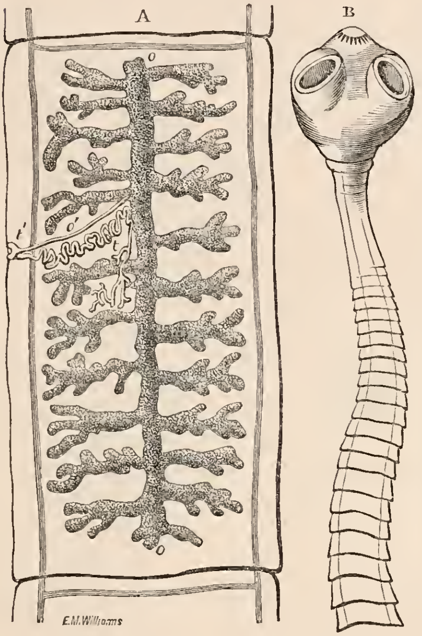
Development of Tænia pistillum of the Shrew.
(From Dujardin.)

a, embryo within the ovum, just about to quit it, with three pairs of hooks; *b*, embryo that has left the ovum, the hooks capable of rapid and extensive movements; *c*, embryo moving freely (of the Tænia serpentulum of the magpie) ; *d*, *e*, very young embryoes of Tænia pistillum ; *f*, *g*, *h*, *i*, different stages of growth of this Tænia ; the separation of the segments gradually increasing, and the development of the reproductive organs in the posterior ones ; *k* (more magnified), the proglottis, or free moving separated segment of this Tænia.

* Von Siebold proposes to substitute the genus Tetrarhynchus for the following five genera distinguished by Dujardin, viz., Rhynchobothrius, Anthocephalus, Tetrarhynchus, Gymnorhynchus, and Dibothriorhynchus. Zeitsch. f. Wiss. Zool. 1850, and Ann. des Sc. Nat. 1851.

The instance already referred to, of the identity of the Cysticercus of the liver of the mouse and rat with the Tænia crassicollis of the cat, and a variety of detached observations which prove that the Bothriocephalus and Tetrarhynchus pass through similar changes from a small Echinococcus-like animalcule to the developed cestoid form, lead to the corroboration of the same general view that the encysted condition of these Entozoa is an incomplete non-sexual embryo or larva, from which, when it passes into the free state, there is formed by a process of transverse

Fig. 27.



Tænia solium. (*From Blanchard.*)

A, one of the longer mature posterior segments with the sexual organs fully developed; *o*, *o*, ramified ovary full of ova; *o'*, the oviduct; *t*, the tubular testis; *t'*, the penis, &c.

B, head, neck and anterior recently formed segments.

fission a segmented individual or compound animal, in which each segment, as it arrives at maturity, attains to sexual completeness. In this process the new segments are always developed between the head and those already formed. If the character of sexual completeness is to be taken as the distinguishing mark of individuality, each segment of the Cestoid may be looked upon as a distinct animal, and the separation of them by transverse fission may be compared to the separation of Medusa individuals from the Strobila polype stock. The Cestoid Entozoa might in the same manner be considered as subject to a peculiar process of alternate generation.

In the preceding sketch of the nature of the reproductive process in the Cestoid Entozoa, I have followed chiefly the views of V. Siebold as explained in the interesting Memoir already referred to. It is right to state, however, that the phenomena have been viewed in a different light by several observers of high authority. Thus, Blanchard and Van Beneden consider the first stage of the Tetrarhynchus-embryo to be a Scolex, in which, after it has been encysted, the Tetrarhynchus is formed: this, according to Blanchard, is its complete condition; but, according to Van Beneden, the so-called Tetrarhynchus is converted into a Rhynchobothrius, and this is in the last place changed into a separate Trematode animal.* Dujardin had previously taken the same view as applied to the separate and independent nature of the joints of the Tænia, which he regarded as individual Trematode animals, and described under the name of Proglottis (see *fig.* 26. *k.*)†; but though there may be some points of analogy between the single segments of Tænia and a Trematode, yet the absence of head, differences in the alimentary canals, and other circumstances, render the correctness of this view, at all events, still doubtful.‡

Trematoda. — These animals, the most common of which are known as Flukes (excluding the Planariæ), comprehend a set of internal parasites of a structure bearing some resemblance to the Cestoidea, but single, that is, not jointed or segmented. The nervous and vascular systems attain to a considerable degree of development: the alimentary canal, which has a mouth but no anus, is in some bifurcated, and in others more or less ramified. The male and female generative organs are united in one individual, and pervade a large portion of the body of the adult animal.

The facts which have been ascertained in recent times concerning the generation of some of the Trematoda constitute one of the most remarkable parts of the history of this process among the Invertebrata. Their general result may be shortly stated thus: — the fully grown and sexual Trematode animal, as observed chiefly in the Distomata, produces ova, which may pass through the earlier stages of their development either in the viviparous or oviparous mode, more frequently the latter. Each of these ova has formed from it an embryo in which no resemblance to the Trematode parent is to be recognised, but presenting the simple structure of a ciliated animalcule like a polygastric infusorian or a Gregarina. This embryo is

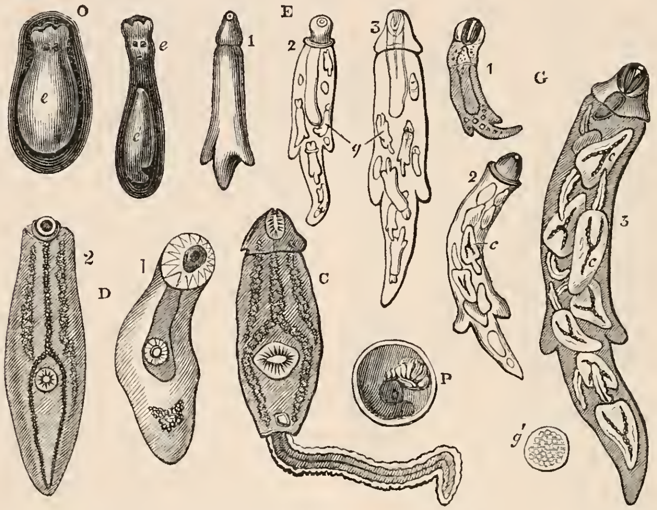
* Bull. de l'Acad. Roy. de Belgique, 1849, No. 1., and Ann. des Scien. Nat. vol. xi. 1849, p. 13.; also a work by the same author on the Entozoa, Brussels, 1850, of which I have only seen an extract in a letter addressed to Milne-Edwards, in the Ann. des Scien. Nat. 1851. tom xv. p. 309.

† Hist. Nat. des Helminthes, 1845.

‡ See also Leblond, in Ann. des Scien. Nat. 1836, and Miescher, Bericht Naturforsch. Gesellsch. Basle, 1840; the Works of Rudolphi on Entozoa; the Article Entozoa in this Cyclopædia, by Owen; Kölliker's Memoir on the Development of Invertebrate Animals, in Müller's Archiv, 1843; Eschricht on Bothriocephali, 1840, &c. &c.

not itself converted by any direct process of development or metamorphosis into a perfect Distoma, but has gradually formed from germ-cells within it a progeny, sometimes of one, more frequently a number of bodies, which, when they arrive at maturity, present each one an external form and internal structure and locomotive powers, entitling them to be considered as independent animals. Nor are these directly converted into Distomata; but again there is formed within the body of each, and in the same gradual manner from germ-cells, a new progeny of animals nearly similar to those producing them and equally differing from the complete Distomata. Each of this new progeny, as it increases in size, has formed within it by development from germ-cells the third progeny of the series, and the last of the cycle; but these are different from their immediate parents, and in their internal organisation soon manifest the type of the true Trematode. These animals are endowed for a time with very active locomotive powers, to which a long caudal appendage contributes; their two progenitors have been confined in the parasitic condition, but these

Fig. 28.



Series of changes in the development and generations of Distoma. (From Steenstrup.)

O, Ovum with embryo or larva developed in it. *e*, this embryo in a free moving state; *e'*, another embryo in its interior. (These are of Monostomum mutabile, from V. Siebold.)

E, this last embryo farther advanced. 1, first stage, soon after it becomes free; 2 and 3, farther on, with *g*, the second generation, within them in various stages.

G, 1, one of this second generation at an early period of its advancement; 2 and 3, farther on, with *c*, *c*, Cercariæ or Distoma-larvæ, within them; *g'*, one of the granular globules from which the Distoma larvæ and previous generations arise near the posterior part of the body.

C, one of the Cercariæ or Distoma larva with its caudal appendage. P, the same, passed into its encysted or pupa state, having previously lost its tail.

D, Distomata. 1, young Distoma immediately after it has quitted the cyst, and has penetrated a short distance into the body of the snail; 2, Distoma found deep in the viscera.

are in general freed from confinement, and move about with great vivacity for a time in the water surrounding the animals which their progenitors have infested. In this state they have long been known as Cercariæ, and as they have been supposed to be the young of Distomata, have attracted peculiar notice among Helminthologists.*

The free Cercariæ are not, however, directly converted into Distomata; but appear always to undergo a previous metamorphosis in a chrysalis state, or enclosed in a pupa cyst. Previous to the formation of this cyst the Cercariæ adhere to, and bore into, the substance of the animal infested by the Distomata; the tail is cast off, an exudation from their own bodies forms the cyst, which encloses them: within this they remain for many weeks, and even months, moving all the while, and undergoing changes of development, by which they are at last converted into the complete Distoma.

The greater number of the observations from which this remarkable process of generation has been ascertained to occur are due to V. Siebold and Steenstrup; but the whole succession of changes has not yet been observed in any one species, and it is to the latter observer especially that the scientific world is indebted for the ingenious combination and interpretation of the scattered

* Nitsch, Beitrag zur Infusorienkunde, &c., Halle, 1817; Bojanus, in Isis, 1818; A remarkable and interesting series of papers by V. Baer, in Nov. Act. Nat. Curios. 1826, vol. xiii.; Rud. Wagner, in Isis, 1834; V. Siebold, in Burdach's Physiol. vol. ii. of German edit. p. 187., or vol. iii. of French transl., p. 32., &c.

observations of previous inquirers, as well as the addition of new facts, from which an almost entire certainty is acquired that the various phenomena do actually succeed each other in the order above stated, and that the occurrence of alternate or intermediate generations in these animals is established.

Von Siebold had in 1835 described in the Monostomum mutabile the development of the first embryo from the ovum in the Gregarina-like or animalcular form, and had shown the next change to consist in the formation within the first embryo of a second body endowed with locomotive power, and independent vitality, and differing both from its immediate parent and from the adult.* V. Siebold, as well as others, had ascertained the Cercariæ to be themselves incomplete animals, and to proceed from others by a process of internal production of a non-sexual kind. Steenstrup therefore directed his attention particularly to trace these Cercariæ on the one hand, in their development into complete Distomata, and on the other, backwards through their progenitors towards the first origin from an ovum. His observations were made principally in three kinds of Cercaria, which, along with their antecedent and succeeding conditions, are found in great numbers in the fresh water snails, Lymneus stagnalis, Paludina vivipara, Planorbis, &c., and which had been previously named Cercaria echinata, C. armata, and C. ephemera. In these, especially in the first, the conversion of an encysted Cercaria by metamorphosis into a Distoma, and the descent of the Cercaria (by metagenesis) through two progenitors, not themselves Distomata, was ascertained, but he did not succeed in tracing these bodies back to their origin from ova. By a comparison, however, of the body formed within the animalcular embryo of the ovum of the Monostomum mutabile, as observed by V. Siebold, with the first progenitor of the Cercaria, to which it was found to present a remarkable similarity, the chain of evidence seemed to be complete, and Steenstrup found himself in a position to announce the general views of alternate generation, which have ever since their first publication attracted the greatest attention, and contributed in a powerful degree to modify and direct the investigation of the generative processes in the lower animals.

To the immediate progenitor of the Cercaria Steenstrup gave the name of nurse (altrix, Amme), in allusion to its nursing or nourishing function, and to the immediate progenitor of this one he gave the appellation of "parent or grand-nurse." These terms may be objectionable, but an unnecessary amount of criticism seems to have been bestowed on them by some writers. They are adopted hypothetically by Steenstrup; they do not appear to withdraw him from the matter-of-fact statement of his observations; and they seem to be, in many respects, short and convenient terms in the description of the phenomena. These bodies have in the Cercaria echinata all the appearance of distinct animals, that is, a body with a head separated by a neck or collar, a tail or caudal projection, and two processes of the integument similar to limbs, a mouth and alimentary cavity, and they move with all the appearance of spontaneity; but it ought to be remarked that the form and powers of these nursing or formative cases differ considerably in various other species, and in some present so little of the external form or endowments of an independent animal, that the more general appellations of germ-cases, or germ-sacs, or sporo-cysts, may be more appropriate to them.*

It is chiefly among the aquatic Gasteropod Mollusca, and a few land ones, that these observations have been made; but V. Siebold has extended them to some of the Trematoda inhabiting the air-sacs and other parts of water fowls, which no doubt come from the same Mollusca, and obtain access to the seat of their final parasitic habitation from the water or along with food, into which they have come as Cercariæ, after having previously been parasitic in the Mollusca. It is easy to understand how the ova of the Distomata discharged from the bodies of the water fowl may gain their place in the Mollusca. V. Siebold has observed in a very interesting manner also the passage of the Cercariæ into the bodies of water insects (larvæ of Ephemera and Perlida), which he placed together with a quantity of Lymneus stagnalis, from the various parts of whose bodies the Cercariæ were discharged in numbers out of their nursing capsules: the penetration of the integument of the insect by the Cercaria and the mode of casting its tail being precisely the same as that observed by Steenstrup in the Mollusca.†

Both these observers agree that the first and second germ-cases (or nurses), and the Cercariæ, or Distoma-larvæ, arise by a process of gradual development from extremely minute granular spherules, which are at first situated in the posterior region of the body, or between the alimentary cavity and the integument. These are certainly not ova: but we are at a loss to state to what class of reproductive germs they may be referred with greatest accuracy.‡

It is known that the bodies which inhabit the aqueous chamber of the eyes of many fishes are imperfect Distomata. Steenstrup has frequently observed these larvæ in the pupa state adhering to the inside, and sometimes to the outside, of the cornea, and he has occasionally noticed a delicate streak through the cornea, indicating the track through which the animal has penetrated; and he considers it as extremely probable that all the Trematoda of the eyes of fishes, of which a vast variety has been described by Nordmann§, are

* See Wiegmann's Archiv, 1835.

* See Victor Carus, über den Generations-wechsel, for a figure of these more simple forms of sporocysts.

† See the Article PARASITES, in R. Wagner's Handwörterbuch der Physiologie.

‡ See *Fig.* 28. *g'*.

§ Mikographische Beitrage, &c., 1832.

at one time encysted, and that of the two principal forms distinguished by that observer, the one is the more advanced and the other is the larva.

From what has already been observed it seems probable that other productions previously described as Entozoa of various kinds, may, in reality, be nurses or larvæ of different Distomata; and that many of these may be brought under their several specific distinctions, when the new paths of investigation pointed out by the suggestions of Steenstrup and V. Siebold have been diligently pursued.

Von Siebold has recently related* a very interesting observation on the remarkable double Trematode animal, discovered and described by Nordmann†, under the name of Diplozoon paradoxum, from which it seems to be ascertained that this double animal is produced by the actual union of two nearly similar simple ones, by a process of partial fusion, which, though much less complete, seems to partake in some degree of the nature of conjugation, such as occurs in the Closterium and some of the lower vegetable bodies. The single animal, first described by Dujardin, under the name of Diporpa ‡, was observed infesting the minnow (Leuciscus phoxinus) in the same streams with the gudgeon (Gobio fluviatilis). This animal corresponds nearly in form and structure with the half of the Diplozoon, with the exception of its smaller size, and the absence of generative organs. On the side of the Diporpa a projecting sucker exists, and the union between two of these animals which gives rise to the Diplozoon, begins by a mere adhesion of this sucker, which becomes more and more complete, so as at last to lead to that entire fusion and combination of the adjacent parts of the intestinal canal and some other organs, which has excited so much surprise in the Diplozoon. The development of the genital organs in both of the two united animals succeeds to this union.

Annelida. — Some phenomena in the reproduction of the Annelida are to be referred to the indirect mode of generation now under consideration. The most of these animals are hermaphrodite; they are all more or less jointed, or formed in the adult of repetitions of segments of similar structure, the anterior and posterior alone differing from the rest. The jointed structure does not exist in the embryo when it first leaves the egg; but is gradually produced by a process of gemmation, which may be styled intervening rather than fissiparous. In the multiplication of these segments the new ones are always formed in the interval between the caudal segment and that which is next to it; the seat of new production differs therefore in the Annelida and Cestoid worms; for in the latter

* Zeitschrift für Wissensch. Zool. 1851.

† Op. cit.

‡ Hist. Nat. des Helminthes, 1845. Dujardin had noticed the resemblance between this body and the two parts of the Diplozoon, and had conjectured that it might be in some way the young of the Diplozoon.

of these animals the new joints are developed at the cephalic extremity, and there is also some difference in its nature, as the multiplication of joints in the Tænia is in some degree truly fissiparous.

A few of the jointed Annelida have long been known to be subject to another kind of development, by which one or more complete segmented individuals are formed close to their caudal extremity, and spontaneously separate to enjoy for a time an independent life. This remarkable fact was first described by Otto Fred. Müller, in the small Nais proboscidea*; and Gruithuisen described accurately the same phenomenon in a Nereis or Chætogaster.† This process was looked upon by these observers as an instance of accidental fissiparous generation; but it has received a different signification and a greater interest from the more recent researches of Quatrefages and Milne-Edwards.

The first of these naturalists observed in a number of individuals belonging to the genus Syllis‡, at a certain period of their life, a new individual to be formed at the caudal extremity of each. The part was first marked off by a notch or transverse groove, the form of the parent individual gradually appeared in it, with the head, eyes, the same joints, limbs, &c., and it was ultimately separated by spontaneous fission. But the resemblance between the original individual and its offspring was chiefly external; for it was found that while the parent animal continued to exercise as before the functions of nutrition it was not possessed of generative organs; and, on the other hand, the new individuals seemed destined alone to perform the reproductive functions, and contained the fully formed sexual organs, while their alimentary canal appeared to become atrophied, and was not employed in the digestion of any newly assumed food. These individuals lived long enough after separation to complete the reproductive process by the formation of fecundated ova.

Milne-Edwards observed in the Myrianida fasciata §, a similar, but more numerous gemmiparous production of sexual individuals. In this animal, as many as six new individuals were observed to be formed in gradual succession, one before the other, and between the caudal and terminal segments of the original body. Each one of these new individuals, as it

* Naturgesch. einiger Wurmarten des Süssen und Saltzigen Wassers, Copenhagen, 1800; and in a Nereis, in Zoologia Danica.

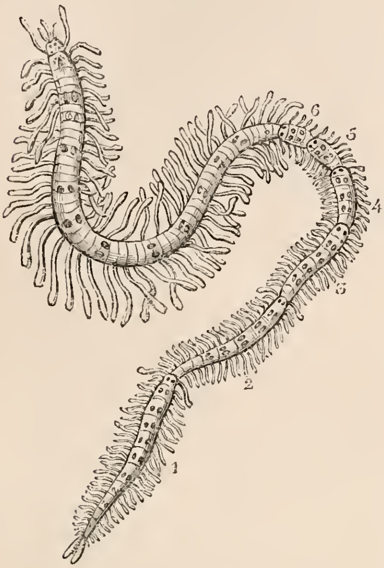
† Nov. Act. Nat. Cur. vol. xi. See also J. Müller's Physiol., by Baly, vol. ii. p. 1424; Owen's Lect. on the Gener. and Develop. of the Invertebrated Animals, in 1849, in Med. Times, vol. xx. p. 83, where he refers also to observations of Oersted in an Eulosoma, and of Schmidt in a tubicolar Annelide, called Filograna.

‡ Annal. des Scien. Nat. 1844, tom. i. p. 22. Otto F. Müller had also noticed the phenomenon in the same animal, and described it under the name of Nereis prolifera, in his Zoolog. Danica, vol. ii. p. 15.

§ Annal. des Scien. Nat. 1845, tom. iii. p. 170. See also Longet's Traité de Physiologie, tom. ii. part 3rd, p. 47.

arrived at maturity, and acquired the external configuration and structure (though of smaller size) of the parent, was found to be possessed of reproductive organs, while the original animal had not acquired any. The first

Fig. 29.



Myrianida fasciata. (*From Milne Edwards.*)

Twice the natural size. At the posterior part of the body are seen six young, produced between the caudal and the next joint in succession, from 1 to 6.

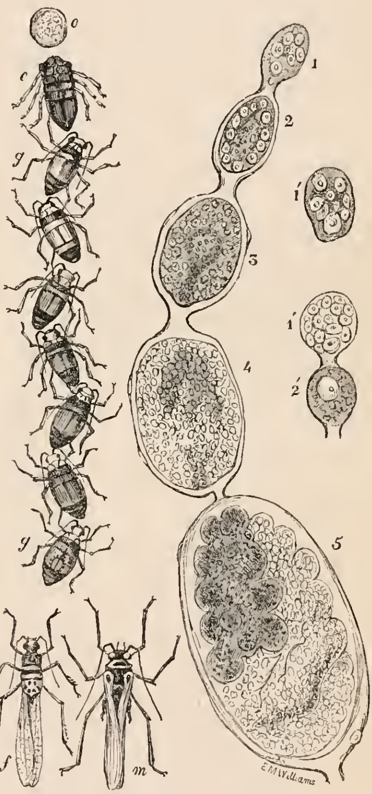
formed was situated farthest back, and remained for the time attached to the original caudal joint, and the others followed in succession before it, the last produced being attached to the terminal joint of the parent body; and each newer individual presented a less developed structure than the preceding one. In the animal observed by M. Edwards, the anterior or youngest individual had only ten rings, the second had fourteen, the third sixteen, the fourth eighteen, the fifth twenty-three, and the last, or caudal one, thirty rings. It would appear, therefore, that the new individuals take their origin from the last joint of the parent Annelide. The observations of M. Edwards farther make it appear that the process of development and multiplication of the segments in each of the new individuals is the same as in the young Annelide first formed from the ovum; that is, the embryo is at first without segments or rings, the head and caudal part existing alone, and the joints being gradually formed between them, and in succession, from the posterior of the segments previously produced.

These phenomena cannot fail to recal to our recollection the production of sexual individuals by a non-sexual process analogous to gemmation from imperfect parents or nursing stocks; and as Mr. Owen has remarked*, "Since the individuals so propagated alone acquire the generative organs, an alternation of generations may here be affirmed of such species; the oviparous individuals producing eggs from which the gemmiparous individuals come, and these, in their turn, reproducing the oviparous individuals."†

But it is to be observed, that in many others of the Annelida, the generation is of the ordinary kind, or consists in the production of sexual individuals, by their direct or metamorphic development from the ovum.

Insecta. Aphides. — A remarkable example of a similar modification of the reproductive

Fig 30.



Production of Aphides.

A. (*After Owen.*) Diagrammatic representation of the succession of generations of Aphides, from the fecundated ovum *o*, the first embryo *e*, the successive non-sexual progenies, *g* to *g* (of each of which only one individual is represented), to the male and female insects, *m* and *f*.

B. (*After Leydig.*) Enlarged view of the chambers of one of the ovarian oviducts of a viviparous Aphis. In the uppermost chambers are seen the fine nucleated cells, of which one in 1′ and 2′, larger than the rest, descends; and in 3, 4, and 5, are seen the changes of this and other granular and cellular blastema, from which the new individual is formed.

* Lectures, 1849, Med. Times, vol. xx. p. 83.

† At the same time it ought to be mentioned in connection with the above, that, according to some

process among animals higher in the scale, but in them of an exceptional character, has long been known to occur in the various species of the common plant-louse, or Aphis, first discovered by Reaumur * and Bonnet †, and confirmed and more fully illustrated by a variety of accurate entomologists in more recent times. In this animal, successive generations, amounting each to a considerable number, and in the Aphis lanigera ‡ averaging about a hundred, are produced for seven, nine, or eleven times, according to the species, from parents of no sex, or rather which seem to possess the structure of females imperfectly developed. The course of the generative process is the following: perfect male and female winged insects are observed only towards the autumn season: these fly about in great quantities, the impregnated females deposit their eggs covered with a protecting case of mucus in the axils and other recesses of plants, where they remain during the winter. In spring there are developed from these ova a brood of larvæ, or imperfect female Aphides, which soon produce, by an act of viviparous generation, and without any concurrence of the male sex, a progeny of a similar kind, and this is repeated, in successive generations, for nine or ten times in the common species, or for ten or twelve weeks during the summer, at the end of which time the last brood brings forth male and perfect female individuals, both of which die after having provided by the production of fecundated ova for the continued generation during the next season.

Upon the discovery of this very remarkable mode of reproduction, various theoretical conjectures were made in regard to its nature; but no satisfactory explanation presented itself, till the knowledge of the general nature of the process of non-sexual larvation came to be brought under a general principle or law. It is now obvious that the production of the successive generations of Aphis-larvæ may be regarded as an instance of the multiplication of individuals from the product of a single ovum, previous to the development of the true sexual organs and the exercise of the sexual functions. But this example of non-sexual larvation deserves attention, not only from its occurrence among animals placed so high in the zoological scale of organisation as insects, but also from the degree of perfection of the larvæ themselves, and from the circumstance that the new broods are formed, not as in the other examples of this process to which the attention of the reader has already been directed, by a division of the whole body, or by gemmation from its external or internal substance, but from germs arising within a determinate organ, corresponding in its general form and anatomical relation, though not entirely similar, to the generative organ of the perfect female.*

The genital organs of the viviparous or larval Aphides differ from those of the perfect or oviparous females, principally in the want of the receptaculum seminis, and the organ which secretes the mucous investment for the ova, and there is also some difference in the form of the ovarium, or germiparous part of the organs.†

The gradual development of the larva brood within the oviduct of the viviparous parent has been traced carefully by several observers. J. Victor Carus has attempted to show that this process is to be distinguished from the usual process of development from an ovum by the absence of cell multiplication, and by the formation of the embryo of the larva from a merely granular germ: but more recently Leydig ‡ has shown that though there may be differences in the structure and mode of development of the ovum and of the viviparous germ, the latter arises as truly as the former from cellular elements. The uppermost compartment of the oviduct contains, according to Leydig, from eight to twelve distinct nucleated cells, together with a quantity of finely granular substance. One of these cells appears to descend into the second compartment, in which an outer layer of cells exists, with finely granular substance internally: in the third compartment the cells of the outer layer have become still smaller and more numerous, and have formed, in fact, a covering to the germ, similar to that which proceeds from cleavage in the ovum. The rudiments of the internal organs now begin to be distinguishable, and the various external organs are successively developed out of the cellular mass. The cellular structure of the ovum of insects is at all times difficult to be traced in the earlier stages of development; and it seems to be established by these observations that the origin of the embryonic structures from cells is at least as obvious in the viviparous as in the oviparous germ (see *fig.* 30. B.).

General Remarks on Alternate Generations.—Having now shortly described the principal varieties of the reproductive process which may be brought under Steenstrup's law of "Alternate Generation," it may be proper to review very briefly their general nature.

recent observations, the parent or stock individuals of both Syllis prolifera and Nais proboscidea arrive ultimately at sexual perfection after having given off a number of sexual individuals by the caudal gemmation. See Leuckart on Metamorphosis, Non-sexual Reproduction and Alternate Generations, in Zeitsch. für Wissensch. Zool. 1851, in which he refers to Frey and Leuckart, in Beitrage zur Kenntniss Wirbellos. Thiere, p. 96; and to Schultze, in Archiv. für Naturgesch, 1849, p. 287, for observations proving this fact.

* Histoire des Insectes, Tom. iii. Paris, 1738.

† Traité d'Insectologie ou Observations sur les Pucerons, 8vo, 1745.

‡ See Owen's Lect. on the Invertebrate Animals, 1843, p. 235.

* It is conjectured by Von Siebold (Vergleich Anat. der Wirbellos. Thiere, p. 634), that the same mode of production may occur also in some kinds of Cynips and Psyche.

† See the interesting observations of Owen, in Parthenogenesis, p. 38., and elsewhere; V. Siebold Vergleich. Anat. and Froriep's Neue Notizen, vol xii. p. 308; and J. Victor Carus, Zür nähern Kenntniss des Generations-Wechsels, Leipzig, 1849.

‡ V. Siebold and Kölliker's Zeitsch. für Wissenschaftliche Zoologie, vol. ii. p. 53.

These phenomena are confined to the Invertebrated animals, and among them are to be regarded as occasional and exceptional rather than general. Among the Protozoa they may exist to a greater extent than is yet known; they occur more or less in all the divisions of the Radiata, but more constantly and obviously in the Polypina and Acalepha than in the Echinodermata: among the Mollusca they have been observed only in the comparatively limited classes of Bryozoa and Tunicata: they are almost universal in two divisions of the class Entozoa, viz. the Cestoidea and Trematoda, but they are altogether absent in the Nematoidea; they belong only to the lowest division of the Annelida, and among the Articulata proper the almost entirely exceptional examples are confined to the class of insects. Nor are the phenomena universal in those classes or orders of the animal kingdom in which they have been described. In some of these divisions, therefore, and in all the others of the animal kingdom, the manner of the reproductive process is ascertained to be *direct*, that is, by generation from sexual parents, and by development, or in some instances by metamorphosis, from ova to sexual individuals; to which may be added, in some animals, by the multiplication of like individuals, separate or aggregated, by gemmation. But although this general statement is applicable to the present state of our knowledge, we are still too imperfectly acquainted with many forms of the reproductive process to warrant us in affirming that there may not yet be discovered many other deviations from that which has long been familiar to our minds as the more common and direct connection between the ovum and the perfect or sexual individuals which produce it. In the mean time let us endeavour, according to our present information, to determine the true character of the seemingly exceptional phenomena, of which the more important have been noticed in the preceding section.

The views first suggested by Steenstrup, in 1842, in connection with these phenomena are unquestionably to be regarded in the light of a discovery, and the attempt to deprive them of their character of novelty and importance, or to refer them to other previously known general laws, has entirely failed.* It may be that the smaller portion only of the facts on which the views are founded may have been first observed by Steenstrup, and that parts also of these views may be in themselves premature, speculative, or erroneous; but all discoveries in science are the result of the successive and concurrent observations of a number of inquirers; and no one who has had an opportunity of studying the history of the progress of research into the reproductive function during the last twenty years, will deny that the view which has associated together the phenomena in question under a common principle, has had a most important influence in modifying the doctrines and in guiding and suggesting the researches of those physiologists who have devoted themselves to inquiries into the origin, early conditions, and zoological affinities of the lower animals; and it may truly be affirmed, that no one could at present enter upon the investigation of any obscure or doubtful department of animal or vegetable production among the lower series of these kingdoms of nature, without making especial reference to the views embodied in Steenstrup's generalisation.

The occurrence of non-sexual multiplication among some of the Invertebrated animals had long been known, as of Polypes, by budding, so admirably described by Trembley in his work published in 1744; and of the Aphides, by internal production, discovered by Reaumur and Bonnet; and of the Nais and Nereis, by external extension, described by Otto F. Müller, in 1800; the imperfect conditions of some of the Entozoa had been detected by Nitsch and V. Baer in 1818: the two forms of the Salpæ were known to Chamisso in 1819, who, more than any other observer, appears to have foreseen in these animals the discovery of alternate or dissimilar generations; but the first observations, from which the peculiar nature and general doctrine of the phenomena now under consideration may be regarded as having been deduced, are those of Sars, on the compound Polype stock of the Medusæ, in 1828, and of Rud. Wagner, on the production of Medusiform bodies from a polype (Coryne aculeata), in 1833. From that time, observations followed one another in rapid succession, and continue still to crowd upon us, so as to have changed almost entirely the aspect in which we have been accustomed to regard the development of the lower animals: and it is only necessary to mention collectively the names of some of those whose observations have contributed most to extend and to establish these discoveries in different classes of animals, to exhibit the importance attached to them by zoologists, comparative anatomists, and physiologists of the highest character in our time, such as Dalyell, Lister, Sars, Lovén, V. Siebold, Nordmann, Eschricht, Steenstrup, Van Bénéden, Kölliker, Owen, Dujardin, Milne Edwards, Blanchard, Quatrefages, J. Reid, J. Müller, E. Forbes, Désor, Vogt, Agassiz, Huxley.

The peculiar nature of these phenomena as compared with those of the better known and more common form of sexual generation, consists in this, that in some animals, in all of which, be it observed, the permanence of the species is secured by the sexual production of ova, the body or individual which is developed immediately from the ovum is not, in general, itself the bearer of the sexual organs, but, nevertheless, maintains for a time an independent existence, or presents the structural and functional characters of a separate or distinct individual; these characters often differing remarkably from those of the sexual

* See Ed. Forbes' Remarks, in Treatise on Naked-eyed Medusæ, 1848, p. 83., *et seq.*

individuals from which the ovum derived its origin: and that subsequently this individual, or one or other of its successors, has formed in connection with it, either internally or externally, and without sexual organs, a new progeny, which may consist of one or of many individuals, which have each of them more or less of the structure and properties of independent animals, and which, however variable their other organisation may be, present this in common, that they are sexually complete, and renew the true generative act by the formation of fecundated ova. In some animals it is the immediate offspring of the individual developed from the ovum which resumes the sexual function; in other animals this offspring bears a second brood, or a third, and even more successive generations, before the return is made to sexual reproduction. This process of non-sexual production is, in some instances, very analogous to external gemmation; in some it resembles transverse fission; and in others it proceeds from the interior of the parent body, in a manner which has been called internal gemmation, but which must be considered as different from a true budding process, and cannot, in a few words, be correctly characterised. These deviations, therefore, are peculiar in this, as compared with the mode of reproduction in other animals; viz. 1st, that the immediate product of development from the ovum is not usually itself the producer of ova, but that this function is delegated as it were to the sexual individuals, which are the products of its non-sexual generation; 2nd, that it frequently happens that in place of one individual only resulting from the development of an ovum, several, and even a great multitude of individuals are produced by the non-sexual multiplication of the product of sexual generation; and, 3rd, that while the several series of individuals proceeding from the various successive acts of production, may, in one sense, be regarded as different stages of an animal specifically the same, or are together necessary to make up the species, yet their form, organisation, and modes of life are often so different, that many of them have frequently been described as belonging to different species and genera, or even to different orders and classes of animals; and, but for the knowledge now possessed of their close affinity, as established by their common origin, would still continue to be dissociated from each other in the systems of the zoologist.

The doctrine of alternating generation has not, however, been admitted without reservation by some physiologists. In various parts of his recent admirable work on General and Comparative Physiology, and elsewhere*, Dr. Carpenter has expressed his dissent from the views of Steenstrup, both as regards the existence of an alternation of a true generative process and the alleged *nursing* function of one or more of the series of individuals so produced; and seems disposed in some measure to undervalue that author's researches, considered either as original observations, or as embodying a novel and important generalisation. Dr. Carpenter regards the phenomena in question as analogous to, if not identical with, those of metamorphosis rather than of generation; and we are left to suppose that he does not think the difference essential between such metamorphoses as occur in one and the same individual and those which result in the production of a multitude of dissimilar individuals. According to this view, the new animal produced by the non-sexual process is the result of a process of development or growth, and ought therefore to be regarded as formed by budding or gemmation, rather than by an act of generation properly so called. In a recent paper on the subject of Metamorphosis, Non-sexual Reproduction, and Alternate Generation (Zeitsch. für Wissensch. Zool. June, 1851, p. 170.), Leuckart has advocated somewhat similar views, endeavouring to refer all the instances of so-called alternate generations to metamorphosis; but this obviously requires that we should change the signification usually given to this term. But the restriction of the word generation to the sexual process of reproduction, though it might be convenient and proper, were we now to have to employ it for the first time, seems somewhat arbitrary in this case, as it is contrary to common practice, and physiologists have long been in the habit of making the distinction between sexual and non-sexual generation. No new term has been suggested applicable to, or descriptive of, all the phenomena in question; and I apprehend, that, however desirable the change may appear, we must continue to designate the process of non-sexual production as one of "Generation" in its physiological sense, and the series of new beings thus formed as so many "generations" of individuals in the common or vernacular sense of the term. As Professor E. Forbes remarks, the alternation of forms is admitted, but not the alternation of generations. The bodies produced by one individual, if they assume new forms and move about as separate and independent animals, must be regarded as so many distinct individuals; and if they are different, and if the one produces the other (even though it may be by a process of gemmation), we must admit that they belong to different generations.

The distinction between the formation of a new individual from an impregnated ovum, and that which takes place without the concurrence of sexual organs, is one which, unquestionably, all will feel disposed to regard as most important; but it still remains undemonstrated that all the animal beings which are of non-sexual origin are necessarily formed by a process of gemmation analogous to ordinary growth. It has already been pointed out that the mode of their origin is, so far as it has yet been ascertained, very various; and, at all events, in some of them, there is a wide departure from that which we have been accustomed to regard as an act of

* In the British and Foreign Medico-Chirurgical Review, vol. i. and vol. iv.

gemmation, or simple sprouting of the parent texture. We cannot be too cautious in making wide generalisations in regard to phenomena so various and so imperfectly known as those of alternate or intermediate generation are; and the only safe course in the progress of such inquiries is to apply terms to the phenomena which are no more than the exact expression of what is well ascertained regarding their nature. Now, who that has observed or studied the history of the two states of the Salpians, and the relation in which they stand to each other, can hesitate to admit that two dissimilar generations alternate, and that a different generative process has taken place for the production of each? or who, knowing the relation subsisting between the fixed marine polype and its free moving medusoid offspring, or that between the larger medusæ and their compound polype stocks, would deny to each of these series of beings the attributes of distinct individuals, or regard the productive acts by which they take their origin in any other light than as two dissimilar kinds of generation? But this seems scarcely more than a question of words. It is important rather to notice that while some of the polypes now alluded to multiply their like (that is polype-forms) by budding, their medusoid progeny also occasionally produce their like (or similar medusoids) by gemmation; and surely it is expedient to regard as somewhat different that production of distinct medusoid individuals from a polype stock, which is an advance in its stage of being, and which gives rise to an animal different in structure, mode of life, and functions, from its parent, from that kind of production which is no more than the repetition of the parental form or the extension of its parts.

The term *nurse*, applied by Steenstrup to the non-sexual producers, seems inappropriate, and may, in one part at least of his treatise*, have led him into purely speculative comparisons, such as that with the workers among the gregarious insects; but in other parts of his essay the author's speculative views are kept in strict subordination to the simple description of the facts. Due allowance ought also to be made by the English reader of this work, for the circumstance that, though an excellent translation, it comes to him through the German from its original language. Less objection would probably have been taken to his theory had the term "preparing stocks," or some one conveying a similar meaning, been substituted for that of "nursing individuals."

Professor Owen also, though admitting in the full extent the peculiar and important nature of the phenomena of alternate generation, objects to the term nurse or nursing animal, as calculated to mislead, and holds the views of Steenstrup, embodied in the phrase "Alternating Generation," to be defective, as not affording any real explanation of the nature of the phenomena, or rather, as being no more than a statement of the facts, without referring them to a sufficiently general law or connecting principle.

Professor Owen's attention had been, before 1843, attracted to the remarkable non-sexual multiplication of the summer Aphides, the structure of which he minutely examined, and had been led to the opinion* that the germs from which the offspring of this non-sexual generation arises are the remains of the original germ-substance of the yolk, which have not been applied to the formation of organised textures in the individual immediately developed from the ovum. Professor Owen has given the name of Parthenogenesis, or Virgin-production, to this mode of generation, and in the very able and ingenious Essay under that title, published in 1849, containing the substance of two lectures, introductory to a most instructive course of lectures on the Generation and Development of the Invertebrated Animals, and also in various parts of these lectures†, has communicated a more lengthened exposition of his views. "The progeny of the impregnated germ-cell," says he, "form the tissues, &c., but not all of them are so employed, some of the derivative germ-cells may remain unchanged, and become included in that body which has been composed of their metamorphosed and diversely combined or confluent brethren: so included, any derivative germ-cell, or the nucleus of such, may commence and repeat the same processes of growth by imbibition, and of propagation by spontaneous fission, as those to which itself owed its origin; followed by metamorphoses and combinations of the germ-masses so produced, which concur to the development of another individual; and this may be, or may not be, like that individual in which the secondary germ-cell or germ-mass was included."‡ He states farther, that the lower the animal in the scale of life, the number of derivative germ-cells and nuclei which retain their individuality and spermatic power is greater, and the number of those that are metamorphosed into tissues and organs, less. The simplest animals are nothing more than nucleated cells, or in the minute and microscopic ones, as Gregarina and Polygastria, one nucleated cell only; the middle layer of the wall of the Hydra he describes as consisting of nucleated cells. In Compound Polypes and Parenchymatous Entozoa a large quantity of derivative germ-cells is retained among their textures or other parts; and the same is the case at the caudal extremity of the Nais and young Annelida. Professor Owen informs us that he has observed the germs of the viviparous Aphides in the embryoes near the simple digestive sac before any organs have been formed for their reception, and that when these germs are afterwards included in the tubes which correspond to the ovaries and oviducts, he regards them as comparable to the germ mass in its mi-

* On Alternate Generations, p. 112.

* See Lectures on the Comparative Anatomy of the Invertebrated Animals, 1843, p. 234. and 366.

† As published in the Medical Times, vols. xix. and xx.

‡ On Parthenogenesis, p. 5.

nutest state of division, and as differing from ova in the absence of the germinal cell.* Notwithstanding the attractive ingenuity of these views, and the great weight which all must be disposed to attach to the statements of so accomplished an anatomist, the theory they involve or expound, when fully considered, does not appear entirely to remove the veil from the mystery of alternate generations, nor to afford that satisfactory explanation or generalisation of its nature which might be desired: for it is to be feared that under the appellation of nucleated cells, as applied to the structure of the lowest animals, very various kinds of organised structures have been confounded by authors, and we are certainly very far from having had determined, by actual observation, the nature or source of the minutely granular masses from which what has been called internal gemmation proceeds; and though it may be admitted that most new structures take their origin in masses of blastema, more or less cellular and granular, the relation of these to the germ masses of the ovum are far from being ascertained. It may be granted, that in the case of the first brood of Aphides formed in the non-sexual way from the first individual immediately developed in the ovum, a residuum of germ-cells may have served as the original blastema of their germs; but when we consider the inconceivably minute portions of this that are to pass to the next and to the successive generations up to nine or eleven, we seem to have to deal rather with a theory of the original pre-existence and "encasement of germs" than with a matter that we can ever hope to decide by observation: and in the greater number of the other instances of alternate generation, there is no possibility of tracing the origin of the germs of the new individuals formed by gemmation to the yolk or germ-mass, of which they are regarded as the included remains.

Professor Owen has well remarked †, that "in the Vertebrated, and in the higher Invertebrated animals, only a single individual is propagated from each impregnated ovum. Organised beings might be divided into those in which the ovum is uniparous, and those in which it is multiparous. This is the first and widest or most general distinction which we have to consider in regard to generation, and in proportion as we may recognise its cause will be our insight into the true condition on which Parthenogenesis depends." But this distinction, notwithstanding its acknowledged importance, does not carry us any farther into the insight of the essential conditions of the phenomena by the theory of the residual germ-mass originating new germs; for when the greater part of this mass is converted into the textures and organs of the embryo directly developed from the ovum, there is still as great a difficulty as ever to understand what circumstances should determine a minute residuum, supposing it to exist, to form an entire new individual, or a prodigious multitude of individuals, in place of only an additional portion of texture, or an additional organ, which might more naturally be regarded as the correlative products of their brethern germ-cells; or why, in other numerous instances, in which, to all appearance, an equal quantity of residual germ-mass exists, no such formation of new individuals occurs.

It appears equally fair to suppose that the germs of the ova of all animals must have originated within the ovaries of the female parents from residual germ-cells included in the blastema of these organs; but no distinction has ever been established between that blastema in its primitive state and that of other organs of the body: and there does not appear to be better reason for considering the germs of individuals formed by gemmation, as derived more directly from residual and included germ-cells, than those of the ovarian ova.

I have not adopted the term Parthenogenesis, as applied to the alternate generations, because it implies that this kind of production occurs in female animals. Now, although the observations of Owen and V. Siebold have shown a remarkable similarity to the female structure in the case of the viviparous Aphides, this is altogether wanting in the other instances of alternate generations; and this process is strictly non-sexual rather than uni-sexual in its nature. Were it desirable to change the name for this process, the term "Metagenesis," suggested and sometimes employed by Professor Owen, seems well adapted to express exactly what occurs in alternate generations, without calling for the admission of any hypothesis beyond that of the new production being an act of generation; and it seems to me to be the most exact translation in scientific terminology that can be given of the German of Steenstrup in "Generations-Wechsel." In a convenient shape it is precisely descriptive of that change of form by generation, or by production of a new individual, which it has been my object to show has been accurately distinguished in the general law of Steenstrup, as different from a mere change of form by growth or by metamorphosis in the same individual.

At the same time it is deserving of notice, that, among the compound Polypina, the continuous multiplication of individuals proceeds to such an extent, and with such remarkable regularity, as to give rise to composite masses, often of very large size, the general arrangement of which bears a considerable resemblance to that of plants: and we are led still more to institute a comparison between these animals and plants by the circumstance of the similarity of their continuous growth by the addition of new sets of polype individuals to the extension of the leaves and branches of a tree or ramified plant, and by the correspondence of the occasional formation of sexual individuals on the polype stock

* On Parthenogenesis, p. 38.
† Loc. cit. p. 62.

with the development of flowers. It is not without considerable interest, that the same conditions as to temperature, season, supply of nourishment, &c., seem to determine the one or the other kind of production in both the animal and the vegetable bodies. Many botanists regard the plant as an assemblage of individuals; and zoologists are for the most part agreed as to the distinct individuality of the parts united in a compound polype. But the tendency to spontaneous separation of these individuals, especially in their sexual form, is very frequently exhibited in the animal kingdom, while it is rarely, if ever, met with among plants; and among the polype tribes, as well as in other examples of alternate generation, the striking difference of form, structure, mode of life, and functions, of some of the sexual individuals developed by non-sexual generation, seem to warn us against extending the comparison farther than the admission of the general analogy above adverted to, or, at all events, precludes us in the mean time from drawing any arguments as to the nature of animal production from that which is as yet only imperfectly understood in the vegetable kingdom.*

These considerations raise another question on which recent writers are at issue in regard to the theory of Alternate Generations, viz. whether the various animal bodies formed by the non-sexual process within one act of sexual generation are to be regarded as so many *individuals* composing the species, or whether they are to be considered only as the different states of one and the same individual. I have abstained from entering directly on the discussion of this question, from the desire to avoid the confusion which is apt to arise in it from the use of terms in other than their usual significations. In regard to connected animal forms, such as those which coexist in a Compound Polype, less difficulty might be felt than in those instances in which a complete separation of the progeny from its producer has taken place; but it seems to require a greater departure from the ordinary signification of a common term than is warranted by our present imperfect knowledge of the phenomena, arbitrarily to determine to regard as merely one individual all those bodies which may be formed by a non-sexual process from the product of a single ovum, notwithstanding the great variations in their structure and mode of life, and the complete separation and apparent independence to which they may attain. It is unquestionably important to acknowledge the integrity and permanence of the species as maintained in the midst of all these variations by generation from an ovum; but there does not seem to be any obvious impropriety in the instances in question in regarding the species as made up of individuals differently constituted among themselves, and produced one out of another by a non-sexual process. The term Zöoid suggested by Huxley, or Zöonite previously employed by Milne Edwards and some other French authors, or any such term agreed upon as implying a relation of affinity among the various bodies included in one act of true sexual generation, may perhaps remove some of the ambiguity; but I confess I do not think the present state of the inquiry warrants the total abnegation of individuality to the various animal bodies produced in the non-sexual manner.*

In reviewing, then, the whole subject of Alternate Generation, it seems to be equally premature to refer the whole of the phenomena included under this term, which may hereafter be discovered to be very various in their nature, to a simple process of gemmation or individual development, or to attribute them to the existence of certain powers, such as a germ-force or spermatic power, remaining in certain germ-cells, or to reject altogether the hypothesis of Steenstrup of Alternate Generations, which indeed is little more than the expression of the course of the observed phenomena; until we shall know more exactly the minute structure of the germ from which a bud arises, and the difference between that and the germ of an ovum, and until we shall be more fully acquainted with the whole structure and series of changes of the various animal forms that have been the subject of consideration in the preceding section.

We regard it, therefore, as more consistent with the actual state of our knowledge of the facts to describe the phenomena of Alternate Generation as a peculiar mode of existence belonging to some of the simplest kinds of various classes of Invertebrated animals, which seems to have especial reference to the preparation of the sexual organs; and of this nature, that the animal immediately developed from the fecundated ovum does not usually arrive at sexual completeness, but has formed from it, by a non-sexual process of production, another individual of a different form, or a succession of them, which finally attain to sexual completeness, and produce the fecundated ova that originate the generative cycle; and the effect of which is, to render two or more successive generations of dissimilar animals necessary to the completion of the species to which they belong.

* For farther remarks on this subject the reader is referred to an account of vegetable production, under the Article Vegetable Ovum.

* Some acute and interesting remarks by Mr. Huxley on this subject will be found appended to a sketch of J. Müller's discoveries on the Echinodermata, in the Annals of Natural History, 1851, vol. vii. p. 1. I would also refer at this place to the Lectures of M. Agassiz on Comparative Embryology, Boston, 1849, as presenting a most engaging view of the influence which the study of the metamorphosis of animals, along with the history of alternate generations, must exercise on the systematic views in Zoology and Comparative Anatomy, and I also take this opportunity of referring to some remarks by Mr. C. Spencer Bates in a paper on the Development of the Cirripedia, in the Ann. and Mag. of Nat. Hist. for 1851, vol. viii. p. 331. for a statement of the relations subsisting between the various forms of animals considered in their sedentary and free states, either in individual species or in different genera or families of the various classes of animals.

Additional Remarks. — Since the foregoing observations on alternate generation were printed in August, 1852, the knowledge of these peculiar phenomena and of the whole forms of reproduction in various classes of animals has been considerably augmented by several important contributions. A short reference to some of these researches seems necessary in this place, in order to complete our notice of the phenomena referred to.

The statements of Stein, referred to at p. 7 of this article, as to the encysted condition of the Vorticellæ previous to their undergoing multiplication, having been called in question by Ehrenberg*, the subject has been farther investigated by F. Cohn, with the result both of a full confirmation of Stein's statements, and of its being ascertained that a considerable number of other infusoria are subject to a similar change; among which he mentions species belonging to the genera Euglena, Prorodon, Chilodon, Notophyra, Trachelius, Trachelocera, and Stentor.† Stein holds it to be fully established that the nucleus of the Vorticella is its true reproductive organ. From this nucleus a progeny is formed in two modes, in both of which the parent animal becomes encysted. In one mode the encysted Vorticella is converted into an Acineta-form by the prolongation of narrow contractile processes of its substance from the external surface, and from the nucleus of this Acineta-like animal successive single ones are produced by gemmation. In the other form, the nucleus of the encysted Vorticella undergoing subdivision, becomes converted into the germs or spores of numerous new Vorticellæ. This process is probably in these Protozoa the equivalent of a sexual production of ova; and appears to correspond nearly with that which takes place in the production of the Navicella-like progeny from Gregarinæ, with this difference, that in the latter case two Gregarinæ are united or fused together into a sphere previous to the production of the new progeny or spores.

The view of Leydig, therefore‡, that the parasitic infusoria named Gregarinæ are only an imperfect or metamorphosed condition of a Filaria, does not appear to be confirmed.

In reference to the Entozoa, recent experiments have furnished ample confirmation of the views now adopted by almost all physiologists, that these animals are the product of a true sexual generation, and that their ova, or embryoes, or larvæ, are introduced from without into the bodies of those animals which they parasitically inhabit; while at the same time the knowledge of their migrations and remarkable transformations becomes more and more precise from additional and renewed investigation of their different forms.

Herbst, who had previously failed in some experiments to cause the transmission of the Trichinæ of the muscles by implantation in wounds of animals, at last succeeded in 1850–51 in causing the muscles of several young dogs to be infected with these parasites by giving them to eat the flesh of a badger which had lived with him for some time in confinement, and in which the Trichinæ existed in great quantity.* About the same time Kuchenmeister found that by causing young dogs to swallow along with their food a quantity of the Cysticercus pisiformis (of the hare and rabbit), the intestines of these animals were in a few weeks invariably occupied by a Tænia (T. serrata). Von Siebold, who, as has before been remarked, was the first to advance the opinion (in 1844), that the Cysticercus fasciolaris inhabiting the liver of the rat and mouse is only the early condition of the Tænia crassicolis of the intestine of the cat, has with the assistance of Lewald performed a series of experiments of a nature similar to those of Kuchenmeister, which have established beyond doubt that various kinds of Cysticerci, and also the Cænurus of the sheep's brain, and the Echinococcus veterinorum, are always converted into Tæniæ or Cestoid Worms within a short time after they have been transferred, as by feeding, into the alimentary canal of suitable animals. These experiments have also afforded to V. Siebold the means of observing in a most interesting manner the process of development and gradual conversion of the cystic into the cestoid entozoon.†

Since the publication of V. Siebold's experiments, farther researches on the same subject have been laid before the Academy of Sciences of Paris by Van Beneden and by Kuchenmeister, in Memoirs presented by them in competition for the grand prize offered by the Academy in 1853 for the scientific investigation of the Development and Transmission of Intestinal Worms.‡

The observations and experiments communicated by Van Beneden in this prize essay, and those contained in his highly interesting Memoir on the Cestoid Entozoa, published in the Mémoires de l'Académie Royale de Belgique for 1850, have also established in the most satisfactory manner the relation between the encysted or scolex condition and the cestoid form of the Tetrarhynchi; facts which have also been in part confirmed by R. Wagner.§ Van Beneden has observed the first development of the ova of the Tænia dispar of the Rana temporaria ‖ into the small embryo provided with its three pairs of boring hooklets, and has watched with care the active motions of these instruments, by which

* Bericht of Berlin Acad. for 1851.

† Zeitsch. für Wissen. Zool., vol. iv. p. 253.

‡ On Psorospermia and Gregarinæ, in Müller's Archiv. for 1851, translated in Quart. Journ. of Micro. Science.

* Ann. des Sc. Nat., 1852, tom. xvii. p. 63., and in Quart. Journ. of Micro. Science, No. 3. p. 209.

† Zeitsch. für Wissen. Zool., vol. iv. pp. 400. 409. See particularly Plate xvi. A. Also in Annal. des Sciences Nat., 1852, and L'Institut., No. 974.

‡ See the Report of the Commissioners, by Quatrefages, in Comptes Rendus for Jan. 30th, 1854. p. 166.

§ See extract of a letter in Ann. des Sc. Nat. for 1853, vol. xix. p. 179.

‖ Comptes Rendus, 1853, p. 788., and in Annals of Nat. Hist., vol. xiii. p. 157.

the minute embryoes, scarcely larger than the blood-discs of the frog, penetrate into the tissues or organs in which they afterwards become encysted; thus affording the most direct proof from observation of the manner in which the young of these parasites become established in the internal parts of animals. The head, with the circle of hooklets and the four suckers, is then formed at the anterior part of the embryo, constituting now the scolex of Van Beneden; and this author proposes to give the name of proscolex to the previous embryonic stage. In connection with the formation of the head of the encysted animal, it may also be noticed that Stein has observed the three pairs of embryo hooklets remaining for a time irregularly scattered over the enlarged vesicular part of the body.* When the encysted animal (Cysticercus) has been introduced into the stomach and intestine of a suitable animal, generally a carnivorous one, it resists the digestive action of these organs, but speedily loses its caudal vesicle, and gradually acquires the new joints which are formed from the head. It is thus brought to the condition of the strobila, if we choose to liken the jointed state of the tape-worm to the multiple or divided polype stock from which medusæ are thrown off; and lastly, as the sexual organs become fully developed in each of these joints, beginning in the posterior ones, which are first formed, these are detached one by one, and constitute in the separate condition the bodies named proglottis by Dujardin and Van Beneden. The latter author regards these as alone the perfect animals of the Cestoid, the jointed strobila being only a preparing stock; and he adheres to the view, previously referred to in this article, that each proglottis approaches in some degree to the organisation of a Trematode animal. According to the views of Van Beneden, therefore, the different stages of a Cestoid worm are the following:—1st, the ovum; 2nd, the first embryo or proscolex; 3rd, the cysticercus, or encysted vesicular body, or scolex; 4th, the jointed stock, tape-worm, or strobila; and 5th, the separate sexual individuals, or proglottides.

Among the Trematode animals the production of a succession of new progenies by a process of internal non-sexual generation has received full confirmation. Van Beneden has added the important fact, however, that some of the Trematoda are not subject to any process of alternate generation or metagenesis. He has traced the whole process of direct development of the animal from the ovum of Udonella caligorum, a viviparous Trematode with large ova. The alternating generation belongs, according to him, to the Oviparous Trematoda, in which the ova are of small size.

In reference to the Compound Medusoid Animals, Siphonophora and Physsophorida, it appears from the researches of Leuckart, Kölliker, Gegenbaur and others*, that the several joints of the connected chains of these animals, as previously conjectured by Milne, Edwards, and others, may fairly be regarded as distinct, though imperfect individuals, some of which are destined for the sexual production of ova, while the free or floating polypine stock remains destitute of sexual organs. The free polypine stock is first developed from the fecundated ovum, and acquires its one or two swimming vesicles: from it there is afterwards formed the long chain of smaller bodies connected together by an extension of the digestive cavity and external substance of the animal. Some of these form swimming bells or vesicles with prehensile and stinging filaments; others are digesting cavities or stomachs, and others, most frequently those last formed in the chain, contain one or other of the sexual products, either male and female among the individuals of the same stock, or distinct sexes on separate stocks. But there is sometimes a combination of the motor and nutritive with the reproductive organs in the same individuals of the chain, which warrants fully their being regarded as something more than the mere repetition of organs belonging to one animal. They are, in fact, the same as the sexual individuals of a compound polype; and in some rare instances indeed they have been observed to become detached and to swim about in the separate condition.

In connection with the alternating generation of the Salpæ, in the discovery of which the whole series of facts now under review may be said to have originated, some doubts were in the previous part of the article stated to prevail as to the relation of the sexes in the animals of the aggregated chain. These doubts have now been in a great measure removed, and the knowledge of the whole phenomena of the reproductive processes in these remarkable animals greatly extended by the researches of C. Vogt† and of H. Müller.‡ From these researches it appears that while, as was previously known, the Solitary Salpæ are entirely non-sexual, the animals united together in the aggregated chain, formed by successive gemmations from one spot of each solitary individual, are hermaphrodite, or possess both male and female sexual products. The ova, however, according to Vogt are developed at a much earlier period than the spermatic substance: indeed, they are advanced to the condition in which they are ready for fecundation, while their producers are still attached as a chain to their solitary gemmiparous parent. The spermigerous organs only advance to perfection after separation; and the process of fecundation must therefore be effected in the animals of the attached chain by the

* In observations made on encysted non-sexual round worms, and the encysted condition of a cestoid inhabiting the Tenebrio molitor, and its larva, in Zeitsch. für Wissen. Zool., vol. iv. p. 206.

* Zeitsch. für Wissen. Zool., vol. iv. p. 304., and vol. v. p. 285. &c.; and Kölliker's Memoir on the Siphonophora of Messina. Leipzig, 1853.

† Bilder aus dem Thierleben, 1852, p. 59.

‡ Zeitsch. für Wissen. Zool., 1853, p. 329.

spermatic matter derived from detached chains which are frequently floating near them. To this result, no doubt, the currents of water in the respiratory cavity will materially contribute.

Since the publication of the first part of this article, the general aspect also of the questions involved in the facts referred to has undergone revision by several authors. The whole doctrine of alternate generation has, it appears, been called in question by Reichert, in a programme entitled Unisexual Reproduction*, which I have not had an opportunity of seeing. In his recent very able and instructive treatise on Reproduction in the Handwörterbuch der Physiologie, Rud. Leuckart†, though he retains the name of alternate generation as designating the phenomena referred to, gives the doctrine little place, and seems still inclined to regard this mode of production rather as a peculiar modification of growth than as a true generation. He is perhaps right in his remark‡, that physiologists have been too much disposed to separate the phenomena of alternate generation from other forms of production of a non-sexual kind, of which he considers them as only a variety; the alternation of different forms being, according to him, only a subordinate and not an essential phenomenon. In his recent very interesting work on Animal Morphology, Victor Carus§ has allowed more importance to the views of Steenstrup, adopting at the same time Owen's term Metagenesis, as most suitable for the designation of this kind of production. This author appears to me to have made the nearest approach to a correct appreciation of the nature of this process in its relation to the whole phenomena of animal reproduction as at present known.

Reviewing therefore finally the whole of the facts and opinions on this subject, I am inclined to adhere to the views expressed in a previous part of this article, that the phenomena of alternate generation or metagenesis ought to be grouped together, and to retain their place as constituting one of the general forms of reproduction among animals; consisting, as they constantly do in a certain number of animals, in the combination, alternation, or succession of the sexual and non-sexual production of individuals all proceeding originally from the development of one ovum. At the same time it is to be noted, that this mode of production does not exist in all the species or genera of those tribes of the lower animals among which it has been observed to occur, and that in some it passes by gradual transitions into other forms of the generative process. It is not on that account the same as them. Metamorphosis and Metagenesis, also, as V. Carus remarks, may be combined, but they are different. "Larvæ, the subjects of metamorphosis, arrive at the state of perfection by throwing off provisional structures which belong to their larval condition, but nurses, the subjects of metagenesis, are themselves entirely provisional structures."

Generation, therefore, or the production of new individuals belonging to a species, may be either of the sexual or of the non-sexual kind. It is only in the Protozoa that the distinction of sex has not yet been discovered. In all other animals the production of new individuals of the species is the result of the development of ova fecundated by spermatic matter. In all the Vertebrate animals and in the majority of the Invertebrate, the development of the ovum gives rise to a single new individual; in most of them by a continuous process of formative growth, in some by successive stages, or by metamorphosis. In a few Invertebrate animals the development of the ovum gives rise directly to more than one individual by what may be named primary division of the ovum. In a considerable number of Invertebrate animals the production of new individuals sexually perfect is not immediate from the fecundated ovum, but secondary or intermediate by non-sexual formation from a preparing stock which is the product of development from the ovum. In such animals an alternation of sexual and non-sexual formation of individuals is necessary for the completion of the act of generation or the reproduction of the species. In a few of these animals only one new individual is formed; but in by far the greater number the product is multiple, thus leading to a great increase in the number of individuals, either in the distinct or in the aggregate form, which have all derived their origin from a single ovum. It is to be observed however, that in some instances the alternating generation may co-exist either with the non-sexual mode of multiplication or with direct sexual reproduction.

In conformity with these views of the relation of the product of generation to the ovum and its progenitors, there might thus be established the following modes of reproduction among animals—viz.

I. Monogenesis, reproduction without known sexual distinction.

II. Digenesis, bisexual reproduction.

III. Metagenesis, alternation of sexual and non-sexual reproduction.

In each of these main forms of the reproductive process the following varieties might also be distinguished—viz.

1. With single progeny.
2. With multiple progeny.
3. By consecutive development.
4. By metamorphic or interrupted development.

* Die Monogene Fortpflanzung. Dorpat, 1852.

† Article *Zeugung*, in the 5th and 6th parts of vol. iv. of Wagner's Handwörterbuch, 1853.

‡ Loc. cit. p. 979.

§ System der Thierischen Morphologie. Leipzig, 1853.

PART SECOND.

Of the Ovum previous to the Commencement of Fœtal Development.

I. Anatomical Structure, Chemical Composition, Origin and Formation of the Ovum in Man and Animals.

§ I. Preliminary and General Comparison of the Ova of Animals.

At a time when the analogy and difference in the structure and functions of the ova of various animals were less known than at present, and especially before the discovery of the true mammiferous ovum, the phenomena of development were almost exclusively observed in the eggs of birds; and consequently in the progress of investigations on this subject, and their extension to other animals, the nomenclature of parts of the egg, and the interpretation of the phenomena of development, came naturally to be founded on those which had previously been adopted in the study of the egg of the common fowl. In more recent times it has been found that the egg of birds presents in some measure exceptional characters, as compared with that of the greater number of animals; and it has thus become apparent that the close limitation of our observations to the class of birds, fruitful as they are universally acknowledged to have been in most important and interesting information on our subject, might tend even to retard in some degree the establishment of the more general laws of typical structure and formative change, which constitute so remarkable a feature of the result of modern embryological researches.

Still, the convenience of being able to obtain the egg of the bird without trouble in all stages of advancement, the familiar knowledge that has so long been possessed of the phenomena of incubation, the proportionally large size of the embryo, the difficulty, on the other hand, of making serial examinations of the ova of mammalia, and, though numerous and important, the comparatively fragmentary nature of the observations in this class, and especially in the human subject, make it desirable that we should not too soon depart from the practice, which has so long prevailed, of making the bird's egg the main foundation of our description of the ovum and formative process in general. But, at the same time, the exceptional structure of the fowl's egg alluded to renders it proper for me to present here, in a connected form, some account of the principal differences among the ova of various animals; so that we may, in some measure, avoid drawing false analogies, or deducing supposed general laws, which may be premature, or may be rendered inadmissible by the existence of ascertained individual peculiarities, or more extensive differences among various classes of animals.

In the commencement of this treatise (p. 3.), the ovum of animals has been described as consisting in general of two sets of parts, of which the one is formed in the ovary of the female, and the other is superadded to the first after it has left the place of its formation. The first, constituting the ovarian ovum (or ovulum of some authors), consists essentially of, 1, the external vesicular covering, or vitelline membrane, 2, the yolk or vitelline substance, and 3, the germinal vesicle, with, 4, its nucleus or macula. As being the most constant in their structure and relations, and the more immediate seat and agents of the formation of the embryo, these parts may be regarded as the essential and most important structures of the egg. The other set of parts, which are subject to great variation in different animals, and are only remotely connected with the formative process, consist chiefly of external coverings of more or less density, either membranous or calcareous, within which often is enclosed some portion of albumen or albuminous fluid along with the ovarian ovum. They serve the purpose, in oviparous animals, of protecting the ovarian egg from the hurtful influences of external agents, and, in rarer instances, of supplying additional nourishment to the embryo; in viviparous animals these parts (as in the chorion of mammalia) serve more important ends, being the more immediate means of establishing that intimate organic connection between the parent and embryo, by which a continual supply of materials for the growth of the latter, is transmitted into its body. From analogy, the outermost covering of the ovum of all animals has generally been termed the chorion.

In thus stating the general structure of the ovum of animals, a certain amount of uniformity, analogy, or correspondence in their several parts has in the meantime been assumed; and the best ascertained facts seemed for long, indeed, to have warranted such an assumption. It will be for after consideration to determine how far the comparison of the several parts of the ova of different animals proves their uniformity of structure and relation. In some instances it may appear difficult or impossible to discover the correspondence; and we must therefore be careful not to be led by the attractive nature of a great generalization, to confound a merely functional or physiological analogy, with an anatomical, a structural and relational identity.

Without entering at present into a detail of the observations bearing upon the foregoing view of the general analogy in structure and function of the ova of animals (which in truth would involve the history of almost all the more recent researches on the subject), it seems proper at this place to call the attention of the reader to the most prominent modern discoveries which have laid the foundation of a more accurate acquaintance with the structure of the ovum, and have also led to the application of improved histological views to the study of ovology.*

* It is not intended at this place to refer to the history of discovery in the department of our subject which includes embryological development, in which

The first modern discovery, which introduced a far greater accuracy into the study of ovology than existed previously, was unquestionably that of the germinal vesicle in the ovarian ovum of birds, by Purkinje, of Breslau, in 1825 *, an observation which led directly to the ascertainment of the general fact that such a vesicle exists invariably in the ovarian ovum of all animals. The extension of this discovery to a variety of oviparous animals, we may consider as due, in the first instance, to Von Baer and R. Wagner.

The next important discovery in chronological order, which contributed, in an eminent degree, to remove one of the greatest difficulties in our subject, was that made by Von Baer, in 1827, of the minute ovum of mammalia, or true viviparous animals. † The discovery of the nature of the mammiferous ovum was rendered complete in 1834, by the observation of the germinal vesicle first by Coste and somewhat later but independently by T. Wharton Jones ‡; and the knowledge of the mammiferous ovum was greatly extended and confirmed by the observations of G. Valentin and Bernardt, of Breslau. §

The nature of the germinal vesicle itself next attracted the attention of ovologists, and a farther addition to the knowledge of its structure was made by Rudolph Wagner, of Göttingen, in 1835, by the discovery in it of a minute particle or mass of fine granules, to which he gave the name of macula germinativa, or germinal spot.* The subsequent researches which that author instituted on the earliest condition of the ovula in the whole series of animals, contributed, more than any others of the same period, to establish the doctrine of a general uniformity in the structure and mode of origin of the ova of animals.† Although it appeared, from the researches of R. Wagner, and has been made still more apparent from late observations, that in several classes of animals the germinal macula loses its determinate form and is subdivided and diffused, as it were, in the germinal vesicle, yet the more circumscribed form of this body, in its earliest condition, and its general prevalence, as a constituent part of the vesicle in almost all animals, seem to indicate the analogy of that vesicle with the true nucleated cell of other parts of the animal body.

After the general nature and structure of the ovum had been ascertained by the several discoveries now mentioned, numerous and important researches followed one another in rapid succession, giving greater extent, minuteness, and accuracy to, and in some instances modifying and correcting, the knowledge previously acquired. Among the authors of these researches, besides those already mentioned, the names of Rathke, J. Müller, Prevost and Dumas, Barry, Reichert, Bischoff, Kölliker, and Vogt, occupy the most prominent place. Of these, and others, more special mention will be made in the progress of our history of the ovum and its development. But, as my present object is to place before the reader only the principal discoveries which may be regarded as the groundwork of the scientific knowledge of our subject, I will only farther call attention at this place, to the influence which the ob-

Malpighi, Wolff, Döllinger, Von Baer and Pander took a prominent part, but only that which belongs to the structure of the ovum itself.

* This discovery was first announced in a small work, entitled Symbolæ ad Ovi Historiam ante Incubationem, Auct. Joann. Evang. Purkinje; printed at Leipzig in 1825, on the occasion of the celebration of Blumenbach's Semisecular Jubilee. A second edition in 4to, with two lithog. plates, appeared in 1830. Purkinje is also the author of the Article *Ei* in the Berliner Encyclopædisches Wörterbuch, in 1834.

† See the Epistola de Ovi Mammalium et Hominis Genesi, Auct. Car. Ern. De Baer, published in 4to., at Leipzig, in 1827; and the interesting Commentary on or Supplement to the same in Heusinger's Journal; and the translation of both of these writings in Breschet's Répertoire d'Anatomie et de Physiologie. 4to. Paris, 1829. As I shall have occasion to return to the history of this discovery, I will not enter on farther details here; but it is right to state that Messrs. Prevost and Dumas may in some measure be considered to have shared in the merit of the discovery; as, in an extended and highly illustrative series of experiments, instituted by them as early as 1824, they were led to the conclusion that the ovules of mammiferous animals, of extremely minute size, were really contained in the Graafian follicles previous to conception; and they even appear to have twice seen in the contents of very advanced follicles, a small spherical body which could be no other than the ovule. See Annal. des Scien. Nat., tom. iii., 1824, p. 135. But Von Baer first demonstrated this body with precision, and explained its relations to the follicle, &c.

‡ Coste's discovery of the germinal vesicle in the rabbit, was communicated to the public in the Comptes rendus for 1833; it is fully described in his Recherches sur la Génération des Mammifères, &c.; 4to. Paris, 1834. In 1835, Thomas Wharton Jones read a paper to the Royal Society of London, containing an account of his observations on this vesicle in the mammiferous ovum, made without a knowledge of those of Coste in the autumn of 1834; but this paper was not printed in the Transactions of that year. It was afterwards published in the Lond. Med. Gazette, in 1838, p. 680. This discovery was confirmed and extended by Valentin and Bernardt, whose observations are recorded by the latter in his work, Symb. ad Ovi Mammal. Hist. ante Prægnationem, Vratislaviæ, 1834.

§ See G. Valentin's Handbuch der Entwickelungsgeschichte des Menschen, &c.; 8vo. Berlin, 1835, at p. 14. The part of this work relating to the structure and formation of the ovum, was translated and published by Dr. M. Barry, in the Edin. Med. and Surg. Journal, No. 127.

* The observations of R. Wagner on this subject, were made towards the end of 1834. This discovery was first published in the 1st Edit. of his Lehrbuch der Vergleich. Anat. 8vo., Leipzig, 1834 — 35, pp. 320 and 352, and in Müller's Archiv. for the latter year, p. 373.

† His more extended researches are described in the work entitled, Prodromus Historiæ Generationis Hominis atque Animalium; folio, Leipzig, 1836. With two copper-plates and very numerous figures. These and the researches of Valentin, are, with reference to the ovum, peculiarly interesting and important as the immediate precursors of the Microscopic Researches of Schwann. See also, the Beiträge zur Geschichte der Zeugung und Entwickelung, by R. Wagner; published in the Trans. of the Roy. Bavar. Acad. of Sciences, 4to., Munich, 1837.

R. Wagner is also the author of the Article *Ei* in Ersch and Grüber's Encyclopædie.

servations and doctrines of Schwann, as to the cellular origin and constitution of the textures of plants and animals, published in 1838, have exerted on the progress of ovology and embryology. In accordance with his general views, Schwann regarded the ovarian ovum as constituting an organised cell, of which the vitelline membrane is the outer cell-wall, the yolk substance the contents, the germinal vesicle the nucleus, and the macula or maculæ the nucleolus or nucleoli.* While the observations of Schwann do not present us with any very important new facts as to the structure of the ovum in particular, and although it may be necessary even to modify, in some degree, the view we should now, with our increased knowledge, be disposed to take of its relation to other organised cells of the economy, still it cannot be doubted that the great generalisation matured by this author has exerted, and still continues to exert, upon the progress of discovery and the scientific aspect of our subject, a no less remarkable influence than that which has been apparent since its first promulgation, on almost the whole range of physiological anatomy; furnishing the key to the structure of the ovum itself, laying the foundation of the histological laws of development, bringing a vast amount of observed facts under a consistent doctrine, and stimulating and guiding the embryologist in new paths of research.†

The most important general facts that have been ascertained in regard to the ova of animals may now be stated shortly as follows: —

1. The ova of animals begin to be formed in the ovary of the female parent at an early period of life, and are produced more commonly in vesicular, more rarely in tubular, cavities or ovisacs of these organs.

2. In those instances, in which it has been possible to detect the earliest stages of formation, the ovum appears very generally to take its origin in the form of a minute spherule or vesicle. This soon enlarges, and is converted into a nucleated cell, which forms the germinal vesicle, and this remains as a constituent part of the ovulum, till the latter is about to leave the ovary, or till the first formative changes commence.

3. The vitellus, or yolk substance, begins to be formed a little later. It is gradually accumulated, either in the vicinity of or round the germinal vesicle, in some rarer instances being produced in a separate organ; it consists of an albuminous fluid in which are suspended a large quantity of granules and oil spherules, or of larger corpuscles, having the form of non-nucleated simple cells. The structure of the yolk substance is subject to considerable variety.

4. The yolk substance and germinal vesicle are together enclosed, in the mature state of the ovarian ovum, by an almost structureless vesicular vitelline membrane, which in most animals is formed later than the other parts, in some at an early period, in others comparatively late, and which is not, therefore, to be invariably regarded as a true cell-wall, or as an original part of the ovum.

5. The germinal vesicle presents several of the characteristics of a true organised cell: the macula, or germinal spot, has in many animals the form and relation of a nucleus; but in some, the subdivided structure of this macula, which succeeds in the progress of formation of the ovum, causes it to lose its simple nuclear character.

6. When the ovulum, or ovarian ovum, attains maturity, it generally leaves the place of its formation in the ovary, and about the same time — in some animals before, in others after it — the germinal vesicle disappears, bursts, or dissolves. In the greater number of ani-

* Schwann, after hesitating somewhat whether to regard the entire ovum or the germinal vesicle as a true cell, gave the preference to the above view, chiefly from a consideration of the manner in which the ovum was believed to be formed, and its correspondence, as he conceived, with the invariable and necessary mode of formation of cells in general. These latter views have themselves undergone some modification since the publication of Schwann's Researches, and we shall probably find (as will afterwards be more fully stated) that a study of the structure and mode of production of the ova in a variety of animals, may render it necessary to modify also the comparison of the parts of the ovum to the organic cell, adopting rather the view of R. Wagner and Henle, according to which the germinal vesicle is regarded as the true cell, and the other parts of the ovum as of the nature of superadded structures.

† Mikroskop. Untersuch. über die Ubereinstimmung in der Struktur und dem Wachsthum der Thiere und Pflanzen, von Dr. Thomas Schwann. Berlin, 1839. The interesting Researches of M. J. Schleiden, on the cellular structure of Plants, entitled Beiträge zur Phytogenesis, published in Müller's Archiv. for 1838, immediately preceded those of Schwann; and they may be considered as forming in some measure, along with his, the basis of modern histology: the researches of the latter author were independently made, and an extract of them published in the beginning of 1838, in Froriep's Notizen; and the two first parts of his fuller treatise were sent to the French Academy, in August and December of 1838. An interesting analysis of both these works in the British and Foreign Medical Review, vol. ix. for 1840, made their contents generally known in this country; and an excellent translation of them both by Mr. H. Smith has since been published (1847) under the auspices of the Sydenham Society. It may be observed, however, that the great and important generalisations which Schleiden and Schwann have, with so much merit, established, may in some measure be regarded as the fulfilment or amplification of, and true deduction from, a variety of detached observations, which had been accumulating, in regard to both kingdoms of nature, for some years, more especially after the improvement of the achromatic microscope had given increased facility and precision to the minute examination of the tissues; such as the discovery of the nucleus of the vegetable cell by Robert Brown, in 1831; the discovery of the cellular structure of the chorda dorsalis by J. Müller; the observations of Henle on epithelium, of Valentin on several similar subjects, and of Turpin and Mirbel on plants, together with the observations previously referred to on the ovum of animals itself. But these detached observations had not led to any important general views before the publication of the Researches of Schleiden and Schwann.

mals, it is uncertain what becomes of its substance.

7. In the greater number of animals the ovum acquires some additional parts, such as albumen, external coverings (shell, chorion &c.), in its descent through the passages of the female parent after leaving the ovary; in some animals an external covering corresponding with the chorion is already formed in the ovary.

8. When the spermatic substance of the male parent has come in contact with the ovum, so as to exert its peculiar fecundating influence upon its germinal part — an action which in a few animals occurs before, but in the greater number shortly after it has left the ovary — the first of the series of changes which follows, and is preparatory to laying the foundation of the new being, consists, in almost all animals, in a peculiar process of division, cleavage, or segmentation, which affects either the whole yolk, or a part of it, or that portion only in the vicinity of which the germinal vesicle has before been situated, and in which the rudiments of the embryo afterwards make their appearance. This subdivision proceeds continuously, till the whole germinal part of the yolk is reduced by it to a nearly uniform mass of corpuscles, or structural elements of microscopic size, which generally occupy or are spread over more or less of the surface of the yolk mass within the vitelline membrane.

9. The rudiments of the embryo, and its accompanying organised structures in the ovum, when such exist, are first formed in the centre of a layer of nucleated organised cells, named by Pander *Blastoderm* or germinal membrane, the formation of which results more or less directly from the process of segmentation above referred to. The disappearance of the germinal vesicle when the ovarian ovum arrives at maturity, the influence of fecundation acting about the same time, the process of yolk-segmentation which immediately follows the latter change, and only occurs as a consequence of fecundation, and the formation of the germinal membrane or blastodermic layer of cells, in which the segmentation results, are successive phenomena of change in a fruitful ovum, which undoubtedly stand in some very immediate and close relation to each other; but the exact nature of that relation is still involved in some degree of obscurity. In some animals the process of yolk-segmentation seems either in itself to be a process of rapid cell-formation, or to be accompanied by it; while in other animals (chiefly those highest in the scale), the segmentation is only the immediate prelude to the generation of the true nucleated cells, which afterwards constitute the blastoderm.

10. The centre of fœtal development is coincident with the place of the germinal vesicle in the mature egg, and with the centre of the blastodermic layer of cells; and it would appear, also, that the principal axis of the embryo is coincident with the line of first division of the germinal part of the yolk in the commencement of segmentation: but it is yet undecided what part the germinal vesicle or its nucleus or macula more immediately take in the segmenting process, or in the origination of the true embryo-cells; and in the higher animals, at least, it is still uncertain whether or not these embryo-cells are the direct progeny or descendants of the germinal vesicle, or its nucleus. The germ spot, the centre of the first segmentation, and the centre of embryonic formation, constitute, therefore, a constant point in all animals, which may be termed the germinal centre of the ovum.

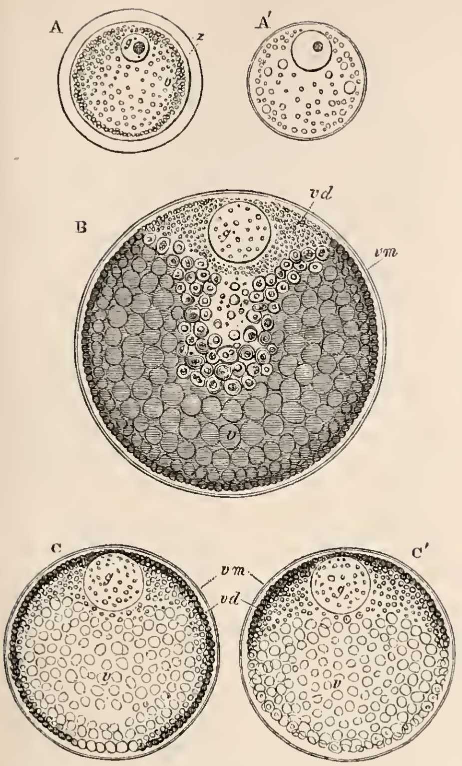
Division of the Ova of Animals into Groups. — Although the researches of modern ovologists thus enable us to assert with confidence the general similarity of structure in the ova of animals, and to point out general features of correspondence in the phenomena which they exhibit in their first origin, progress to perfection, and conversion into the rudiments of the new being; yet it must be admitted that very important differences are also to be observed among various ova, more especially when they have reached a state of maturity. In what has previously been affirmed, therefore, of the similarity of animal ova, it is to be understood that uniformity of a general kind only is implied; and even that correspondence is demonstrated not so immediately, in many instances, by the examination of the fully formed ova, as by their careful comparison, at different stages of their growth, and more especially in their earlier conditions.

The more important of these differences are those which are related to the nature of the germinal portion of the ovum, as compared with the rest of its parts; and a consideration of these differences, in so far as they have yet been observed, appears to lead to a division of the ova of animals into three principal groups, as follows: —

First group. — In a certain number of animals, some of which are viviparous, others oviparous, the ovum is for the most part of proportionally small size, sometimes very minute, as compared with the full-grown parents, and of very simple structure; the yolk substance is entirely composed of elementary granules, or minute and simple spherules; the process of segmentation affects the whole mass of the yolk, and the germinal or blastodermic layer, resulting from that segmentation extends from the first over the whole surface of the ovum; the whole of this layer contributes at once to the formation of the rudiments of the embryo and its accompanying organised structures; the whole yolk, or ovulum, in fact, is germinal, or is converted into the parts of the future embryo. Such is the nature of the ovum in mammalia, and among the Invertebrata, in most Mollusca, Entozoa, Echinodermata, Acalephæ, Polypes, and a considerable number of other tribes.

Second group. — In another set of animals, the great majority of which are oviparous, the ova are proportionally of the largest size; the yolk substance consists very obviously of

Fig. 31.



Diagrammatic representation of the three principal kinds of ovarian ova, in sections (the relation of size not, however, being maintained).

A. Mammiferous ovarian ovum; *z.* zona pellucida or vitelline membrane of some authors; *v.* granular yolk substance; *g.* germinal vesicle, with its nucleus or germinal spot; A′. young ovum of a molluscous animal.

B. Young ovarian ovum of a bird; *v. m.* vitelline membrane; *v.* large yolk corpuscles of two kinds—viz. those of the yellow external part, and those of the cavity; *g.* germinal vesicle without spot or nucleus, but granular diffused maculæ; *v. d.* small granular yolk substance forming the vitelline disc.

C. Ovarian ovum of a batrachian reptile; *v. m.* vitelline membrane; *v. d.* vitelline disc, or formative yolk-substance deeply coloured, and surrounding the large granular yolk substance, in one nearly entirely, in the other, C′, only half round the ovum; *g.* germinal vesicle.

two kinds of organised particles, — viz., of smaller granules nearly similar to those which form the whole yolk in the last group, and of larger cells, usually non-nucleated, and fat vesicles, which constitute the greater part of the mass. The first or granular part of the yolk constitutes a thin disc, limited to one region of the surface, — viz., the upper side in the vicinity of the place occupied by the germinal vesicle, while the cellular substance of the yolk forms the larger spherical mass of the egg. Besides these two, there are also various intermediate forms, which seem to be stages of transition between the other kinds of structural elements. The germinal vesicle in the ripe ovarian ovulum, is situated in the centre of the granular disc, and after its disappearance, the process of segmentation is limited to that disc. The germinal or blastodermic membrane, or layer of cells, extends, therefore, at first, no farther than this granular disc, and consequently it is only a very small part of the ovum which directly contributes to lay the first foundations of the embryo, or its accessory parts; while the larger mass of cellular yolk comes only secondarily to take a part in the process of embryo nourishment. Hence, in such ova, the distinction may be broadly drawn between the germinal or formative, and the nutritive parts of the yolk. Such is the invariable relation of the parts of the ovum to development in the whole class of birds, with some differences in scaly reptiles, in cartilaginous fishes, and perhaps also in cephalopodous mollusca, and a few other invertebrata.

Third group. — In another group of animals the structure and relations of the parts of the ovum are different from, but in some degree also intermediate between, those of the two groups previously described. In this one the yolk, or ovulum, may be stated to be of middle size; its structural elements appear to be of two kinds, — viz., the smaller germinal or formative granules, and the larger, or nutritive corpuscles; but these last are in less quantity, are subject to considerable variety, and exhibit less of the cellular structure which characterises the ova of the previous group. The germinal layer occupies a larger portion of the surface of the yolk than in the large-yolked ova (second group), but in general less than in the small-yolked ova (first group), and its extent is subject to considerable variety; in some, covering not more than a half, in others, extending nearly over the whole surface of the yolk. The segmentation is co-extensive with the germinal part, and more or less of the yolk, therefore, contributes at the first to form the primitive parts of the embryo. Such is the condition of the ovum in the Scaleless Reptiles or Amphibia, and Osseous Fishes. The ova of the higher Crustacea, Arachnida, Insecta, and some other Invertebrata may perhaps be included in the same group.

It will be perceived that in the three groups now mentioned, a distinction has been drawn between a part of the yolk, which is immediately employed in the formation of the embryo, and another, which is only remotely connected with that process. In the bird's egg, it has been stated that the latter part of the yolk is in large quantity, and that in the minute mammiferous ovum the first part only exists, and that in batrachia the two kinds of yolk substance are more nearly equally balanced. This difference among the ova of animals has been long known to physiologists in a general way; but its true nature, as connected with a difference of structure of the two kinds of yolk substance, and their relation to the earliest development of the embryo, has of late attracted considerable attention, and appears to have been first clearly stated by Reichert in 1840, and afterwards in 1843 *; and in accordance with the views of that author, we may with propriety distinguish the formative (or germinal) from the nutritive parts of the yolk. In the fowl's egg, for example (in which it must be admitted these two parts were long confounded together), the cicatricula, together with its so called nucleus, and a part, perhaps, of the lighter-coloured substance which occupies the centre of the yolk and the canal extending from it to the cicatricula, constitutes the formative or germinal part ; and the larger mass of the more deeply-coloured portion of the yolk forms the nutritive vitelline substance. In the mammiferous ovum, on the other hand, the latter part is either entirely absent, or is in small quantity, and the whole of the yolk substance may be looked upon as directly formative, or as analogous to that which forms only the cicatricula of the fowl's egg. Among more recent writers the distinction of these parts has been particularly insisted upon, and illustrated by M. Coste †, and also by Messrs. Prevost and Lebert.‡

The difference in the relative amount of the formative and nutritive yolk substance, as well as in the size of the whole ovum, in birds and mammalia, is manifestly to be regarded as more immediately connected with the different manner in which the embryo is to be supplied with the materials necessary for its growth in the two cases ; in the oviparous mode of development, the whole amount of nourishment required being provided in the egg itself, and detached along with it from the parent ; in the truly viviparous mode, a continual addition of new materials for growth, being made by transmission from the maternal parent in the placenta, or in some analogous structure, which accompanies utero-gestation.

The smaller proportional size of the nutritive part in Batrachia and Osseous Fishes (though most of these animals are truly oviparous), may be attributed to the very early period of development, and consequent small size of the embryo at the time when in these aquatic animals it leaves the egg, and, taking upon itself an independent life, gathers nourishment in the same manner as the adult animal.§

The above arrangement is by no means offered as exhausting the divisions which might be formed of the ova of animals, but rather as bringing forward prominently the most remarkable characteristics of those of vertebrata. It is not improbable that a more accurate acquaintance with the structure of the ova in the animals thus grouped, and more especially of the Invertebrata, may lead to some considerable modifications of the divisions here adopted; but the main distinction upon which they are founded is so important, that even with our present incomplete acquaintance with them, it seems advisable to call attention to it at this place. As I shall have occasion to refer frequently to these groups in the subsequent description of the ova of various animals, in the absence of more appropriate appellations, I will, for the sake of brevity, designate them severally, as follows,—viz., 1st group, *Small-yolked ova*, as in Mammalia ; 2nd group, *Large-yolked ova*, as in Birds, Scaly Reptiles, and Cartilaginous Fishes; 3rd group, *Middle-sized yolked ova*, as in Batrachia, Osseous Fishes, &c.

§ 2. Further comparison of the ova of animals in general, as respects their size, number, form, and the relation of their parts.

Size of ova. — In addition to what has been said on this subject in the previous section, it may farther be remarked that, in the second and third groups, the size of the ova of different genera and species is to a certain extent proportional to that of the adult animal, or of the fully-developed fœtus; but in the first group, or at least in Mammalia, in which the nutritive part of the yolk may be considered as wholly or nearly entirely absent, there is a much greater uniformity in the size of the ova; and, accordingly, the largest mammiferous animal may take origin from an ovum which, when mature, is even smaller than those of species of animals many hundred times less in bulk ; while in the class of Birds we observe the nearly regular increase of the size of the ovum in proportion to that of the parent animal, from the smallest humming bird up to the ostrich, or the still larger egg of the Æpyornis, an extinct bird, of which some of the bones, along with the eggs, have recently been discovered in Madagascar.*

* Entwickelungsleben im Wirbelthierreich; 4to. Berlin, 1840; and in Beiträge zur Kenntniss des heutigen Entwickelungsgeschichte; 8vo. Berlin, 1843, p. 22.

† Cours d'Embryogénie Comparée, tom. i. Paris, 1837; and Histoire gén. et partic. du Developpement de l'Homme et des Animaux, Paris, tom. i. 4to., 1848.

‡ In Annal. des Scien. Nat. for 1844. 3rd Ser. tom. i. p. 193 and 265.

§ At the same time it is to be kept in mind that there are exceptions to these relations, which make it extremely difficult to state any general law of connection between the structure of the ovum and the mode of gestation and place of development of the embryo; as in the case of a few of the lizards and serpents, and some cartilaginous fishes, in which although the egg agrees in general structure with that of animals which are generally oviparous, it is retained in the oviduct or uterus of the female during a part or even the whole of the time of fœtal development; and there are also exceptions in the third group—viz. that of batrachia and osseous fishes as in the Land Salamander and Viviparous Blenny. To this mode of gestation the name of Ovoviviparous has been given. There are many varieties of a similar kind among the Invertebrata, and on the whole it may be stated that there is no constant correspondence between the size of the ovum and the mode of gestation. The Marsupiata also, and the Monotremata among the Mammalia, exhibit interesting modifications, in the first a partial, and in the second, probably a complete residence of the ovum in the uterus of the female parent during development; while the ovum in these animals approaches, in some respects, the type which is more commonly oviparous.

* The circumference of this extraordinary egg

In illustration of the most striking of these differences of size in the ova of animals, the following examples may be referred to: — The human ovum is a body not more than $\frac{1}{200}$ of an inch in diameter; so minute, in fact, that we can scarcely form any estimate of its weight or quantity of matter. Let us assume, what seems probable, that it weighs about $\frac{1}{1000}$ of a grain. Now, if we take the weight of a full-grown fœtus as between six and seven pounds, or 45,000 grains, and the adult human body as about 120 or 130 lbs., or 900,000 grains, it appears that while the full-grown fœtus bears the proportion of one-twentieth of the weight of the adult, the ovum is scarcely a thousand-millionth part. In the fowl, the entire egg, when newly laid, weighs about 2 ounces, or 900 grains, and is nearly one twenty-second part of the weight of the adult body, supposing it to be somewhat under 3 lbs. The chick, produced by incubation, is about 600 grains in weight, or about two-thirds of the egg, and is, therefore, somewhat less than a thirtieth part of the weight of the adult. Again, let us take the weight of an osseous fish (as in a female cyclopterus lumpus recently measured by myself), at 9 lbs. 8 ounces, or 66,500 grains; one of the ova, which were fully developed and filled two enormous ovaries, weighed one-seventh of a grain; and the fœtus of such a fish, when it first leaves the egg, might probably weigh not more than one-tenth of a grain; so that the egg would be in the proportion of 1 to 500,000, as compared with the body of the fish.

It is to be observed, however, that this great disparity of size belongs principally to the nutritive part of the egg, and that there is a nearer approach to uniformity in the size of the germinal vesicle; but in this, too, we shall afterwards see that the size is greatest in the ova of the second group, in which the whole ovum attains the greatest magnitude. In the mammiferous ovum, the germinal vesicle is about $\frac{1}{600}$ or $\frac{1}{800}$ of an inch in diameter; but in the fowl's egg it is of a diameter about ten times greater, and in cartilaginous fishes it is even of a somewhat larger size; but still in no egg does this vesicle depart altogether from that small and almost microscopic magnitude which may be regarded as characteristic of the elementary organic structures.

The size of the ovary, when full of developed ova, is also deserving of notice, as giving some indication of the relative amount of reproductive power in the three groups before distinguished. Thus, in the human species, the two ovaries weigh about 500 grains; in the fowl, when developed at the breeding season, the ovary, with its yolks, may weigh 1,500 grains; and in the lump fish, above mentioned, the ovaries weighed together 3 lbs. and 3 ounces, or 22,300 grains. Thus the ovaries were to the body, in the first, as 1 to 1,800; in the second, as 1 to 13; and in the third, as 1 to 3.*

The following table may serve to exhibit these proportions in a general way: —

Weight in Grains of the —

	Ovum.	Ovaries.	Fœtus.	Adult.
Mammifer -	0·001	500	45,000·0	900,000.
Fowl - -	900·000	1500	600·0	20,000.
Osseous fish -	0·135	22,300	0·1	66,500.

Number of ova. — The number or quantity of the ova which the females of different animals are capable of producing in a given time, or during the whole of their lives, is so various, that only a very vague statement can be made in regard to it. The very great productiveness or fecundity of osseous fishes, and of many of the invertebrata, is well known. The ovary of the herring has been found to contain 25,000 ova. In the Cyclopterus lumpus, before referred to, the number of ova estimated as being contained in the ripe ovaries together was about 155,000; and in the ovaries of a Holibut or Hippoglossus, of 156 lbs. weight, I found about three and a half millions. The queen ant of the African termites is said to lay 80,000 eggs in 24 hours; and the common hair worm, or Gordius, as many as 8,000,000 in less than a day. The Entozoa appear to produce the greatest number of all animals — a fact which is somewhat surprising, when we consider how few of these animals comparatively reach their adult condition. In many of the above animals this enormous production is not a single act, but is repeated again and again in successive seasons.

In birds and those animals belonging to the second group, in which the eggs are proportionally of large size, comparatively few of the ova, of which the germs are visible in the ovaries, come to maturity; and in the natural state only a small number are productive. But it is well known that great variations may be caused in this respect by the condition of the animal; and that in a state of domesticity, and under high feeding, a much greater number of eggs may, in some birds, come to maturity, as in the common fowl, in some kinds of which, indeed, an egg is laid daily for two-thirds of the year — a production which would amount to upwards of 30 lbs. or ten times the weight of the whole animal; and, if

over its long diameter, is stated to have been nearly three feet, and over its short diameter two feet four inches; its greatest length nearly thirteen inches. M. Isidore Geoffroy estimates that it must have contained 10½ quarts of substance, or nearly six times as much as an ostrich's egg, 148 times as much as an ordinary hen's egg, and 50,000 times as much as that of a humming bird. Notwithstanding, however, that in the class of birds there is a general correspondence between the size of the egg and the stature of the adult, this correspondence is not regular or constant, and Prof. Owen has illustrated this fact in a striking manner by reference to the Apteryx of New Zealand, which produces a proportionally very large egg.

* The Article "Zeugung" by Leuckart, contained in two parts of R. Wagner's Handwörterbuch der Physiologie, and which I have only received since the above was written, may be consulted as containing fuller information on the same and the following subject.

the product of different successive years be taken together, a fowl may, at the most, bring forth about 1,200 eggs. I have attempted to count and estimate the whole number of ovula in the undeveloped state to be seen in the ovary of the common fowl, and I find it to amount to 30,000 or 40,000. A great many of these ovula must, therefore, be unproductive in the higher oviparous animals, their germs either remaining undeveloped or being absorbed in the ovaries.

In mammalia, and in the human species, although only a few ovula approach to maturity at a time, and a small number only of the ova, as compared with the whole of those contained in the ovaries, serve for production of the offspring, it is known that a considerable number is discharged from the Graafian vesicles of the ovaries in the unimpregnated state. Thus, in the human female (as will be more fully stated hereafter), one or more ovula are discharged from the ovarian vesicles at every successive four-weekly menstrual period during about 30 years of life, and thus not less than 400 ovula may be excluded from the ovaries; but this number is probably greatly below that of the whole ovula or their germs, which the human ovaries contain; and the ovaries of many quadrupeds present, undoubtedly, a greater number.

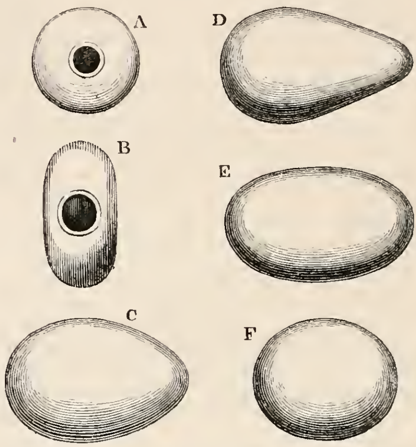
External form and relation of the parts.— The ovum, being composed of cellular, granular, and fluid substance, and being enclosed by an entire vesicular membrane, has generally, at least in its early condition, a spherical form. In the mature state, this form is in many instances retained; but there is also not unfrequently a departure from it, in consequence of the addition of the external parts unequally deposited on the surface of the more globular yolk within them. This spherical form of the ovarian ovum points to its isolated mode of production, and its destination for a separate existence, and is characteristic of the elementary nature of its organic structure.

In the class of birds, the egg is always covered in by an external hard calcareous shell; and in the greater number the external form given by this is somewhat elongated, and not unfrequently, as in the common fowl, with a difference of the size and curvatures at the opposite ends, caused by the manner of the descent through the female passages. There are, however, considerable differences among the different families of birds, as in the nearly globular form of the predaceous, the more elongated form with nearly equal ends in some of the ducks, the well-known shape of the gallinæ and others allied to them, and the greater disparity at the opposite ends, as in the seafowl.*

In those of the scaly reptiles which are oviparous, there is also a firm external covering; but only in some of them, as in most chelonia and in the crocodiles, is there a hard calcareous shell. In the greater number of the sauria and ophidia, the external covering is of a tough membranous or parchment-like consistence, formed of several layers of condensed fibro-albuminous substance, in which either no calcareous matter, or only a small quantity of it, is contained. In those serpents and lizards, again, which are ovoviviparous, the egg, when it descends into the oviduct, is not covered there with the firm external envelope, but with a thinner and softer membrane, similar somewhat to the membrane lining the shell in birds.

* See on this subject the works of Hewetson and others.

Fig. 32



External forms of different eggs of Birds and Reptiles.

A. Batrachian reptile, frog or toad; spherical shape, the dark yolk within, the gelatinous albumen externally; swollen by imbibition of water.

B. Triton or Salamander; elongated external membrane, coloured spherical yolk within.

C. Oval of unequal curves at the two ends, as in gallinaceous, passerine, and many other birds.

D. Very unequal size of the two ends, as common among sea-fowl.

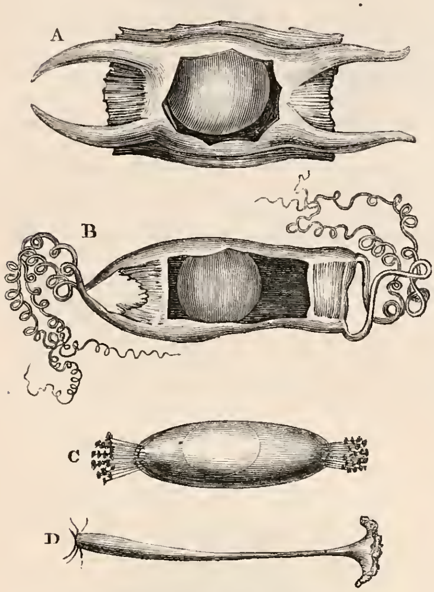
E. Equal oval, as among some ducks, the crocodile, lizard, &c.

F. Short oval or nearly spherical, as in predaceous birds, chelonia, &c.

In the oviparous cartilaginous fishes, a peculiar horny capsule is formed round the yolk and albumen, as they pass through the oviduct at a place where a particular gland is provided for its formation. These capsules are of a fibrous structure, of an oblong, somewhat quadrilateral shape, as in the skate and shark, and, at each angle, are prolonged into tubular processes or filaments, of great length in some sharks, which when short and open, may allow of the passage of water to the embryo contained for a long time within the ovum; and serve also the purpose, when long and convoluted, of entangling and attaching the egg capsule among seaweed and floating bodies.

I have found that in the Myxine glutinosa the globular yolk is enclosed in a horny capsule of similar consistence and structure, but of a simple elongated ellypsoidal shape, and in place of four terminal angular tubes, a number of trumpet-shaped tubular processes projecting from the middle of the two ends, which probably serve the same purposes as the differently shaped appendages of the ova of the shark and skate.

Fig. 33.



External form of ova of Oviparous Cartilaginous Fishes.

A. Ovum of the common skate fish, a portion removed from one side of the coriaceous envelope to show the yolk floating in the white: one-third the natural size.

B. Ovum of the shark, squalus catulus, also opened: half the natural size.

C. Ovum of the Myxine glutinosa, entire: natural size.

D. Enlarged view of one of the 25—30 tubular funnel-shaped processes from the same ovum; the attached end is at D.

In birds, it is well known that the yolk and germ, with their enclosing vitelline membrane, are produced in the ovary, while the albumen, chalazæ, membrane, and shell are more rapidly formed and are added during the passage of the egg through the oviduct. It is by an entirely similar process that these accessory parts are formed in the scaly reptiles, the eggs of which agree with those of birds in the most essential points. The albumen, however, is generally in less quantity and softer, and the twisted chalazæ have not been observed. The membrane which immediately covers the albumen has the same structure as that of the bird's egg; and the calcareous shell, when it exists, as in turtles and crocodiles, is more porous and thinner.

In cartilaginous fishes there is also a glairy albumen investing the yolk, and secreted from the oviduct. In most animals of the second group, or with the large-yolked ova, the vitelline substance consists almost entirely of oily and albuminous matter enclosed in organised cells, the nature of which differs, as previously explained, in the vicinity of the germ and in the other parts of the yolk; this substance contains, besides, the peculiar colouring matter which has given the name to this part of the egg. In all of them a cicatricula exists, which is the seat of the germinal vesicle, and of the first formation of the rudiments of the embryo.

The ovum of the frog, when newly expelled from the oviduct of the parent, consists of the yolk-ball, closely surrounded by a tough layer of peculiar albuminous matter deposited on it in the course of its passage through the oviduct. This substance has the property of imbibing a large, but yet a limited, quantity of water whenever it is immersed in it; and thus, within a short time after the expulsion of the egg from the female, the external substance has assumed a gelatinous consistence, and has enlarged to such an extent as to be on every side equal in thickness to the diameter of the dark-coloured yolk within. I shall have occasion afterwards to state more particularly the important relation which subsists between this process of imbibition and the action of the spermatic substance in fecundation. In the common frog, the ova are thus united in large masses, floating in the water of stagnant pools or rivulets: in the common toad, they are united in long cords, which become entangled among aquatic plants.

In the newts, the external covering of the ovum is membranous, homogeneous and transparent, and of an elongated oval shape, and there is merely fluid intervening between it and the spherical yolk and its membrane; but when the ova are deposited by the parent in the folded leaves of water-plants or other situations, a small quantity of a peculiar glutinous matter, not readily acted on by water, is excreted along with the ova, which serves to fix the ova in a suitable place during the development of the young.* Various examples of a similar kind occur among the oviparous animals of the invertebrata, more especially among insects and mollusca, when the ova are destined to remain exposed, and require protection during a considerable time before development takes place.

In batrachia the yolk is variously coloured in different species: thus, in the common frog, toad, and some others, the surface or germinal part of the yolk is of a black or dark-brown colour, owing to a deposit of pigment granules in the cells of the germinal layer, while the remainder of the yolk internally is grey. In some other batrachia the colour is light brown. In the larger water-newt, or triton, the yolk is of a brilliant light yellow; while in the smaller one, or lissotriton, it is

* See the interesting description of this process by Rusconi, in Amours des Salamandres Aquatiques; Milan, 4to. 1821. I have often confirmed his observations on this process in ponds, and with animals kept in vessels in the house.

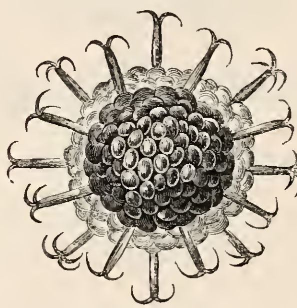
ash-coloured. In the land-newt, which is ovo-viviparous, the yolk is of considerable size, and of a dark yellow, approaching to orange.

In osseous fishes, which are almost all oviparous, the ovule receives, apparently in the ovarian capsule itself, before leaving that cavity, an external covering (or chorion) of considerable firmness. This membrane appears to consist of a substance deposited on the external surface of the vitelline membrane, and becomes coagulated under the action of water; so that its density increases greatly after the ova are deposited, while it is separated at the same time from the yolk by the imbibition of water. The ova are in spawning either deposited separately, or are united in chains or bundles, and in some less common examples* in peculiar nidamental structures, more after the manner of some of the mollusca. The structure of the ovarian ovule, or yolk, and its relation to the germ, differs somewhat from that of the batrachia; for while in the latter animals the yolk substance consists of granules and cells of nearly uniform size, and the germinal layer covers the greater part of the surface, in osseous fishes this layer is more circumscribed, not extending at first over more than a third, or, at most, a half of the yolk, and the remainder of the yolk, which contains a much greater quantity of transparent fluid than in most other vertebrate animals, presents almost invariably a peculiar heap or mass of large oil globules, which float to the upper part of the fluid below the germinal layer.†

The minute ovula of mammalia, when they have reached maturity in the Graafian capsules of the ovary, are nearly spherical bodies, of from $\frac{1}{120}$ to $\frac{1}{300}$ of an inch in diameter, and consist of a mass of finely granular yolk substance, more loose in the interior and more dense towards the surface, and enclosed in a thick firm and transparent vesicular envelope, the vitelline membrane, or so-called zona pellucida. While still within the Graafian capsules, they occupy a situation near the most projecting part of the capsule, or towards the external surface of the ovary, being there imbedded in a layer of granular cells, the *discus proligerus* of Von Baer, which lines the ovicapsule, and lies on the exterior of the clear coagulable fluid with which this capsule is filled. A portion of this lining membrane of granular cells, remains adherent to the ovum after it leaves theGraafian capsule, and has passed into the Fallopian tube; but as it descends towards the uterus, these cells gradually loosen and fall away from the surface of the ovum, the zona pellucida or vitelline membrane of which is thus finally left free. In the farther progress of its descent, there is formed, in some mammalia at least (rabbit), on the surface of the zona by a new deposit, in others, perhaps, by conversion of the zona itself, the external membrane of the ovum, which at a later stage constitutes the chorion. But, in accordance with the destination of the ovum in this tribe of animals for true utero-gestation, this external membrane has then no longer the character of mere inactive limitation of the exterior of the ovum, or defence from injury, which belongs to it in the lower animals; but it becomes an organised and growing texture of active functions, which is the more immediate means of uniting organically the blood-vessels of the mother and fœtus, in such a manner as to allow of the transmission of nourishment from the one to the other.

Varieties of form of the ova among the invertebrata are too numerous to allow of their being described in this place. In the greater number, an external envelope, besides the vitelline membrane, exists; but it must be admitted, that there are some in which these two coverings cannot be distinguished. In some, as in insects, arachnida, polypes, &c., the chorion, or outer surface, presents peculiar markings, ridges, tubercles, or long spines, and is strong and opaque; in others, it is

Fig. 34.



Ovum of Cristatella mucedo.
(From Turpin, Annal. des Scien. Nat. 1837. tom. vii.) Showing peculiar spinous projections from the outer shell.

smooth, delicate, and transparent, so as to allow the whole internal structure of the ovum to be seen through it, and thus to afford most favourable opportunities of witnessing the early changes of development. In most of the invertebrata the germinal part of the yolk covers the whole, or a considerable part, of its surface; they present, however, great varieties of colour and structure, and may, probably, belong to various modifications of the second and third groups before distinguished.

It does not appear that any essential difference has yet been observed in the structure of the ova of those animals which are subject to alternate generation, and those of animals in which the adult form is directly developed from the ovum.

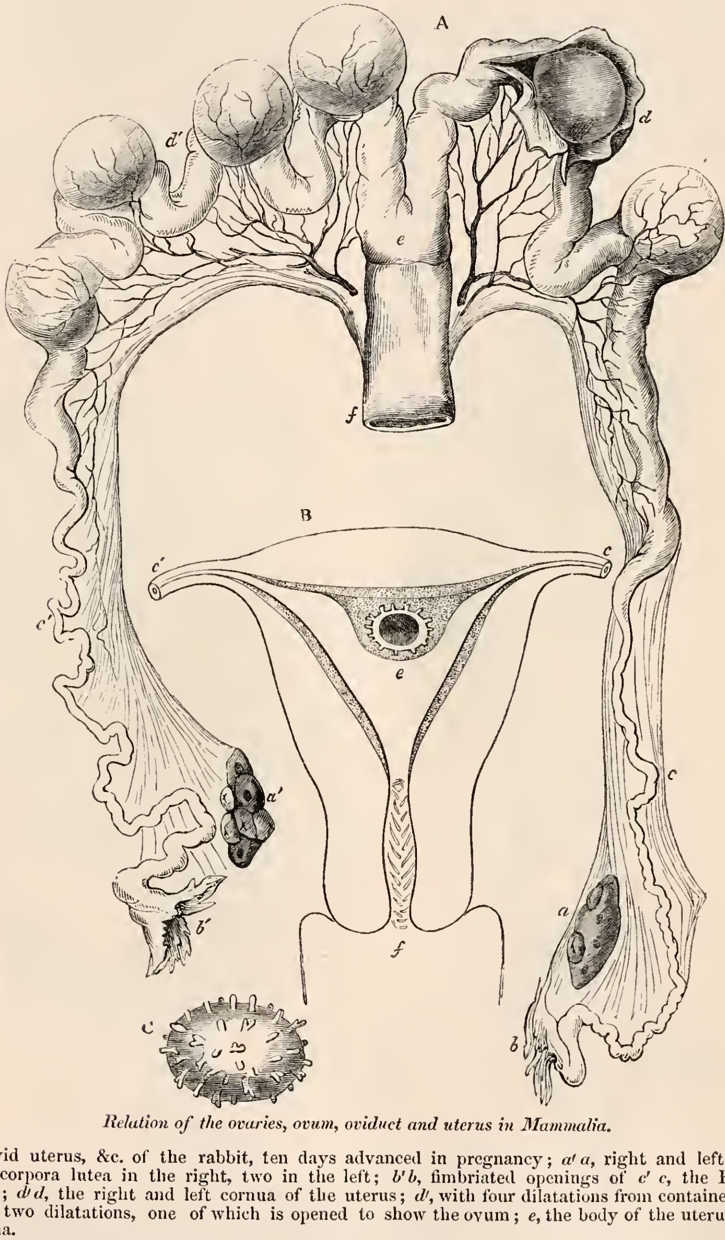
§ 3. Of the ovary in general as the formative organ for the ova of animals.

* As Gobius. See Prof. Owen's Lectures on the Compar. Anat. and Physiol. of Vertebrated Animals, part i. p. 304. A. Hancock on the Nidification of the Gasterosteus aculeatus, &c., in Annals of Natural History, Oct. 1852.

† See a paper by Dr. Davy on the chemical properties of the vitellus of Osseous fishes in Trans. Roy. Soc. for 1851.

The name of ovary is in all animals applied to the organ, however varied in its structure and relations, in which the ova are formed. As already indicated, however, it is to be observed, that in the higher animals, it is only the ovule, or yolk, with its germinal vesicle and enclosing membrane that is formed in the ovary, while the external or cortical parts of the ovum are added to these in their descent through the female passages after leaving the ovary. There are some examples in which it would appear that the whole

Fig. 35.



Relation of the ovaries, ovum, oviduct and uterus in Mammalia.

A. Gravid uterus, &c. of the rabbit, ten days advanced in pregnancy; *a′ a*, right and left ovaries, four corpora lutea in the right, two in the left; *b′ b*, fimbriated openings of *c′ c*, the Fallopian tubes; *d′ d*, the right and left cornua of the uterus; *d′*, with four dilatations from contained ova, *d*, with two dilatations, one of which is opened to show the ovum; *e*, the body of the uterus; *f*, the vagina.

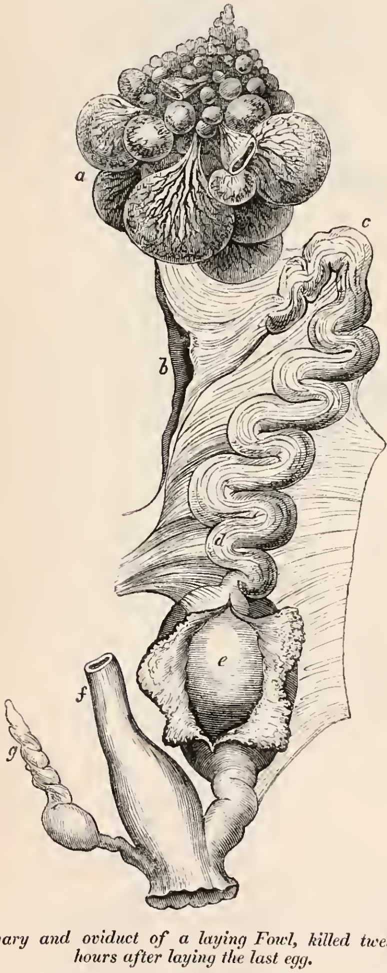
B. A diagrammatic transverse section of the human uterus, at twelve or fourteen days after conception, somewhat less than the natural size; *e*, the uterine cavity, near which the ovum with its villous chorion is involved in the substance of the decidua indicated by the dotted shading; *c′ c*, the Fallopian tubes cut short, by one of which the ovum had previously descended while still of small size.

C. Enlarged view of the exterior of the human ovum, of twelve or fourteen days after conception, showing the villi of the chorion projecting from its surface.

formative process of the ovum, including the addition of the external coverings, is completed within the ovary; and, on the other hand, there are a few instances in which, as in the trematoda and cestoid entozoa, the germinal vesicle and yolk substance of the ovule are formed in separate organs, instead of in the usual manner entirely in the ovary.

The varieties of the ovaries in different animals may be considered under two heads —viz., 1st. Their relation to the passages or outlets as influencing the mode of discharge of the ova from them; and 2nd, their internal structure as related to the form of the ovum produced.

Fig. 36



Ovary and oviduct of a laying Fowl, killed twelve hours after laying the last egg.

a. Left ovary; *b*, opening of the infundibulum of the oviduct; *c, d*, glandular portion of the oviduct; at *d*, the isthmus; *e*, an egg in the uterine portion of the oviduct, in which the shell is begun to be deposited; *f*, the rectum, ending in the cloaca; *g*, the undeveloped right oviduct occasionally met with.

a. Relations of the form of the ovaries to the discharge of ova.—In the majority of vertebrated animals the ovary or ovaries are quite detached from the conducting tube or oviduct; the ovules are formed in close capsules of the ovary, by the bursting or fissure of the wall of which they escape; the oviduct opens at its upper end into the abdominal cavity, and there receives the ovum which has been discharged from the ovary. This is the general arrangement in mammalia, birds, reptiles, amphibia, and cartilaginous fishes. There is some difference in the form of the ovary in the higher and lower of these animals. In mammalia and birds, in chelonia and the crocodiles among the reptiles, and in cartilaginous fishes the ovary is more or less solid, and the ovules are developed in capsules which project towards the external surface; but in the lizards

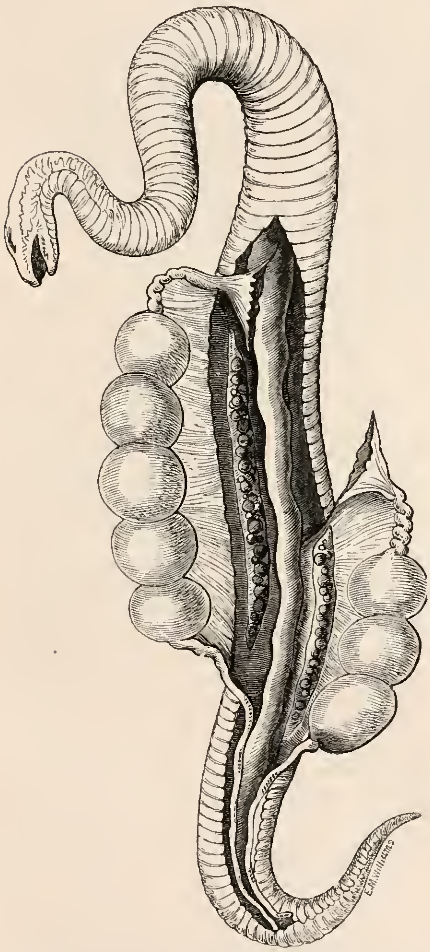
Fig 37.

(*From Carus and Otto.*)

Female of the Falco buteo opened, showing the left larger oviduct and ovary, and the smaller right oviduct and ovary. *a' a*, the right and left ovaries; *b*, the left infundibulum; *c, d*, the left oviduct; *f*, the rectum, ending in the cloaca, which has been opened, showing at *h' h* the openings of the right and left oviducts, and at *i' i* those of the ureters; *g*, the vestige of the right oviduct.

and serpents, and in the batrachia, this organ is hollow, and the capsules in which the ovules are formed burst in dehiscence into an internal cavity, whence the ovules escape into the abdomen by the rupture or opening of the sack of the oviduct, generally at one, but sometimes, as in the frog, at a greater number of places. In the higher animals, in which the ovules escape from the external surface of the ovary, their entrance into the oviduct is in general secured by the temporary apposition of the dilated upper end or infundibulum of the oviduct to the ovary, or the capsule containing a ripe ovule; in the other animals, in which the ova come from the interior of the hollow ovary, the apposition of the oviduct does not appear to be so direct, and there are various other means by which the ova, when they have escaped into the abdominal cavity, reach the open extremity of the oviduct.

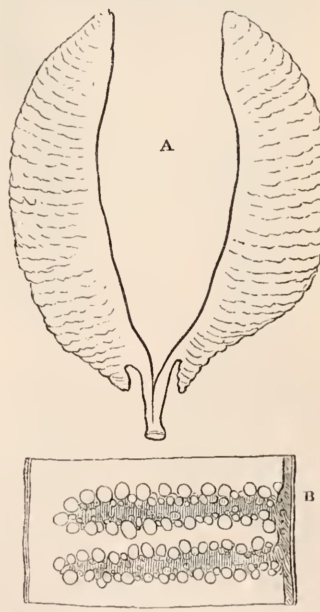
Fig. 38.



Common adder, in which the ova have descended to occupy both oviducts, five in the right, and three in the left: the infundibulum is shown in each oviduct; *a′ a*, the right and left ovaries, each forming a sac, opening anteriorly near the infundibulum for the discharge of the ova, which, when ripe, fall into the interior of the sac, and thence pass into the oviduct.

It is in the class of fishes that the transition occurs from the higher to the lower type of organisation of the ovaries and oviducts. In all of them the ovules are formed in ovarian follicles, and escape by dehiscence from these follicles; but there are several modifications of the relation between the oviduct and ovary among them. 1st. In the sharks and rays, as already stated, the arrangement is nearly similar to that existing in higher animals. The ova, which are of large size, come to maturity singly, or in small numbers at once: on being discharged externally from the ovarian capsules, they pass into the oviduct, and there receive a considerable addition from this organ. The majority of them, as previously stated, are oviparous, and in them a hard covering is formed by a peculiar glandular organ connected with the oviduct; in a few which are ovoviviparous, as the common dogfish, torpedo, &c., the external covering of the ovum is membranous and soft. 2nd. In the sturgeon and in the lamprey the oviduct is very short; still, as it opens superiorly into the abdominal cavity, the relation may be considered the same as in the previous examples. 3rd. In the genus salmo and in

Fig. 39.



Ovaries and oviduct of an osseous Fish.

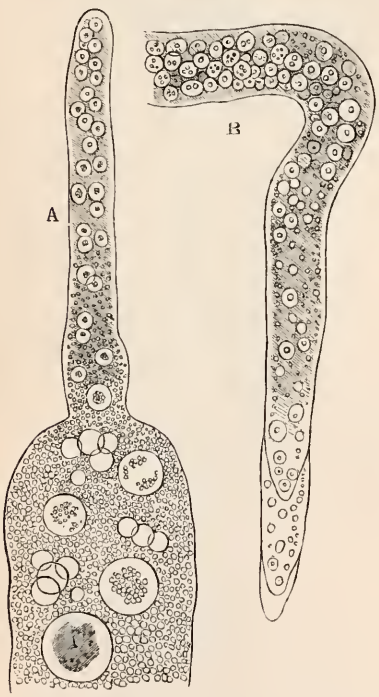
A. Sketch of the two largely developed sacculated ovaries of an osseous fish, with the short oviducts proceeding from near their posterior extremities.

B. Diagrammatic section of a portion of the ovarian sac, showing two of the ovarian plates, from which the developed ova hang in small pediculated vesicles or ovisacs.

the eel among the osseous fishes, the oviduct is entirely wanting, and the numerous ova, which are discharged by external dehiscence from the ovary into the cavity of the abdomen, escape from that cavity by an orifice (porus abdominalis) situated on each side close to the anus. 4th. In other osseous fishes, the ovary and oviduct are united, or the ovary forms a saccular organ, in the interior of the wall of which the ovicapsules are situated, occupying a variable extent of it in different genera ; and the wall of the oviduct, usually very short, is continued from that of the ovary to the outlet from the animal's body. The ova, therefore, which drop by internal dehiscence into the cavity of the ovary, pass directly out by the short oviduct in the laying of the spawn. Most osseous fishes are oviparous; but in a few, as the viviparous blenny, the anableps, paecilia, and some siluroids, the ova, on escaping from their capsules into the cavity of the ovary, remain there during the development of the embryo.

In the invertebrate animals there are very many varieties in the form and relations of the productive and conducting parts of the female generative organs. Three principal varieties may be distinguished among them 1st. A form similar to that just now described as generally prevalent among osseous fishes, in which the ovary and oviduct are continuous, but in which the ova, being formed in ovarian capsules, are dropped by dehiscence into the upper part of the oviducts. Such is still the structure in cephalopoda and some other mollusca. 2nd. A form in which the oviduct may be said to be, as in the last, continuous with the ovary, but in which there is no true dehiscence of the ovules from ovarian capsules, as they are formed at once in the internal cavities of the ovary, which directly open into, or are mere prolongations of, the oviducal tubes. In this form the oviducts may be considered to stand in the relation of excretory ducts to the ovarian glands. In many of this class the ovaries present very various forms ; in some the continuity of the ovarian and oviducal tubes is very obvious and simple, as in the nematoid entozoa, insects, &c. ; while in others, the ovary is more complex and racemose, and the oviducal tubes comparatively simple. 3rd. That form in which the ovaries are variously disseminated over the body of the animals, and in which there are no true oviducts, but the ova escape on various parts of the internal or external surface of the body.*

Fig. 40.



Oviduct and ovary in a continuous tube in Insects and Entozoa.

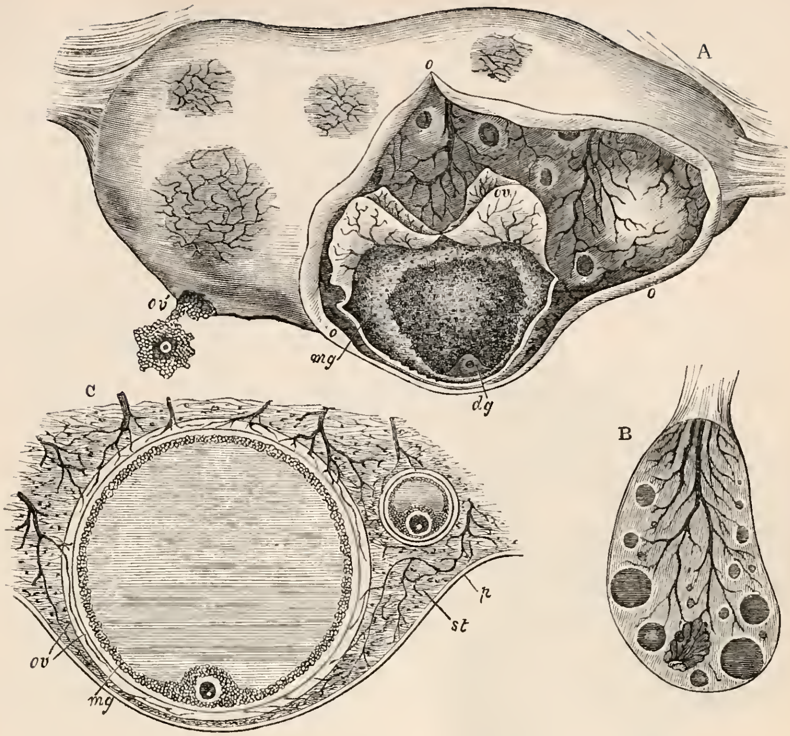
A. (*From R. Wagner*). Upper part of the oviduct or ovary of the Acheta campestris.

B. (*From H. Nelson.*) Upper part of the oviduct or ovary of the Ascaris mystax. In both of these figures the germ-cells and germinal vesicles, with their nuclei, are seen surrounded by the granular matter which afterwards collects round them as vitelline or yolk substance.

b. Structure of the ovaries themselves, as related to the production of the ovula.—In mammalia these organs consist of a pair of solid oval flattened bodies, attached by intervening fibrous tissue to the posterior surface of the broad ligaments of the uterus, and are covered completely, excepting at this attached part, by peritoneum. Below this serous covering there is also a layer of firm fibrous tissue, or *tunica albuginea.* The internal substance, or parenchyma, or stroma, as it has been called, consists of a firm basis of fibrocellular texture, of considerable vascularity. The fibres, as well as the blood-vessels of this substance, radiate principally from the attached border of the organ towards the opposite, or free side, and the rest of the surface. The ovicapsules, or so-called vesicles or follicles of De Graaf, in the human ovary, are situated in this stroma; and at or after the period of puberty are found of some size ; a variable number, from twelve to thirty, or more, being of from $\frac{1}{20}$ to $\frac{1}{6}$ of an inch, and a few even a little larger. These membranous vesicles, filled with fluid, are situated chiefly towards the surface of the free side of the ovary. A larger number of undeveloped capsules, of minute size, also exist in the

* See Von Baer's Entwickelungsgesch. der Thiere ; Owen's Lectures on Invertebrate Animals, 1843, and on Fishes, 1846 ; Rathke (on Development of Fishes, &c.), in Geschichte der Thierwelt, Th. 3.; J. Müller (on Sharks), in Mem. of Berlin Acad. 1842 ; John Davy (on the Torpedo), in Philos. Trans. for 1834 ; and the works of Von Siebold and Stannius, R. Wagner, Carus, and others on Compar. Anat. See also in this Cyclopædia, the articles Monotremata, Pisces, Reptilia, and Organs of Generation.

Fig. 41.



Relation of the ova and ovaries in Mammalia.

A. (*From Coste, as reduced by Longet.*) Human ovary, enlarged four diameters, partially dissected at *o o o*, to show the Graafian follicles in the ovarian stroma: one of these, more advanced, has had its double tunic, *o v*, cut into and reflected; the granular membrane, *m g*, has also been partially opened, showing the thickened portion or granular disc, *dg*, in which the ovum is imbedded near the most projecting part. At *o v'*, another Graafian follicle has been burst, and the ovum in its granular disc is seen expelled from it.

B. Transverse section of human ovary, to show the general arrangement of the developed Graafian follicles towards the surface; twice the natural size.

C. Diagrammatic representation, in section, of two Graafian follicles, in different stages of advancement in the ovary of a mammifer, enlarged about ten diameters. *p*. Peritoneal covering of the ovary, *s t*, ovarian stroma; *o v*, the two layers of the ovisac; *m g*, membrana granulosa, near which is the discus granulosus, with the ovum imbedded.

stroma; and it has been observed, that these are present from a very early period in the ovaries, as first noticed by Carus, and since by myself and others in the child at birth.

The more developed of these ovi-capsules are enclosed by a strong theca or membrane, consisting of two layers; the external thinner and firmer, of a fibrous and vascular structure, the internal thicker and softer, of a fibro-cellular structure and also of considerable vascularity. The capsules are filled with a fluid nearly transparent, which coagulates under the action of heat; and inside the theca, or lining it and covering the fluid, there is a layer of nucleated cells united together in the form of a soft, easily-lacerated membrane, somewhat like an epithelial lining of the capsule. It is in this cellular layer (*tunica granulosa* of Von Baer) that the ovum is placed, being situated in the thicker portion of it (*cumulus proligerus*), directed towards the surface of the ovary.

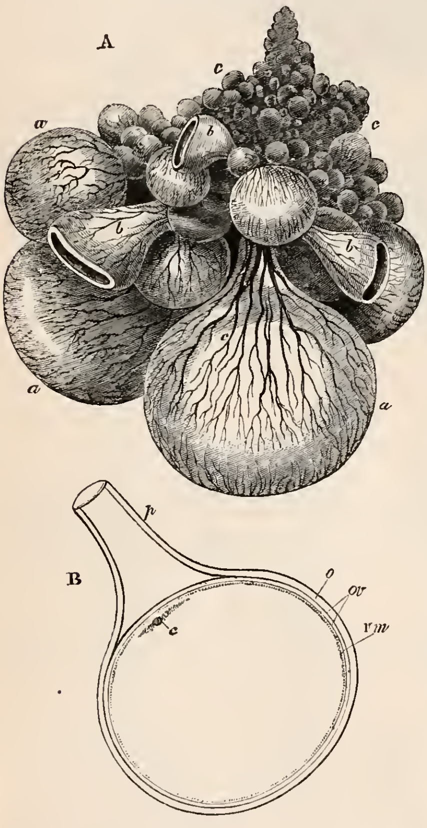
When one of the ovicapsules and its contained ovule has reached maturity, which takes place in one or more of them at regularly recurrent periods, besides the swelling of the ovicapsule itself from the increase of its fluid and other causes, the stroma of the ovary between the capsule and the surface undergoes considerable thinning, and the ovicapsule comes thus to project more immediately from the surface of the ovary. An increased vascularity is also apparent in the same situation; and finally a small circumscribed fissure near the middle of the most projecting part occurs, allowing the escape of the ovule and the granular layer and fluid from the ovicapsule.

The ovule, surrounded by a portion of the cellular layer in which it was embedded, is received by the open fimbriated extremity of the Fallopian tube.

The empty ovicapsule now undergoes a remarkable change by the deposit in its interior of the substance termed corpus luteum, the quantity and nature of which vary greatly according as the escape of the ovule is followed or not by pregnancy. Of this change more will be said hereafter. The result in both cases is the ultimate closure and obliteration of the ovicapsules.

In birds, scaly reptiles, and cartilaginous fishes, the greater size of the ovules when in a state of maturity is connected with a modification of the structure of the ovary and the ovicapsules.

Fig. 42.



Relation of the ova to the ovary in Birds.

A. Ovary of a fowl, showing at *a a a* the most developed ova hanging from the ovary in their pediculated capsules; the non-vascular bands are seen on their most projecting sides; at *b b*, the empty capsules or calyces of ova that have been previously discharged; at *c c*, the more compact part near the root of the ovary, where the ova are less developed.

B. Diagrammatic section of one of the most advanced of the capsules; *o*, the extended ovarian substance forming the capsule; *p*, its pedicle; *c*, indicates in this and the preceding figure the most common position of the cicatricula or germ-disc and vesicle; *o v*, the two layers of the ovicapsule or ovisac, into which the blood-vessels penetrate: the dotted line *v m*, marks the vitelline membrane.

Previous to the age for breeding, the ovary of birds — in which animals only one ovary and oviduct is usually developed or attains to functional activity — is a solid organ of a less firm texture than that of mammalia, and is adherent to the vertebral column in the middle of the dorsal region. It contains at an earlier period a much greater number of ovicapsules of a considerable size than are perceptible in mammalia. The stroma or ovarian substance is in less proportion, therefore, to the ovicapsules and ova.

As the ovules become more developed, they increase rapidly in size; and we then perceive that they bear a different relation to the ovicapsules from that which has previously been described in mammalia, as they fill completely the ovicapsules, and there is no fluid or loose cellular layer between the outer surface of the vitelline membrane and the lining membrane of the theca.* As some of the yolks approach maturity their increase in size is proportionally much greater, and the theca or ovicapsule, and along with it the ovarian substance, is distended in like proportion; and in this manner the ovary of the fowl at the breeding season has lost its appearance of compactness or solidity, and seems to be composed almost entirely of a larger number of pediculated ovarian capsules of the most various sizes, filled with the yolks or ovules in all stages of development. Nevertheless, a little attention shows the solid part of the ovary still remaining at the part attached to the vertebral column, forming the ground, as it were, from which the pedicles of the enlarged capsules spring, and containing still a very large number of minute undeveloped ovules in their correspondingly small ovicapsules.

The large ovicapsules of the developed ovary of the bird consist of two layers, which are loosely united together by blood-vessels and binding tissue towards the pedicle and over the greater part of the capsule, but are more firmly knit together at the free border. At the latter place the blood-vessels of the theca, which are on all the other parts distributed in wide or comparatively large channels very thickly set, suddenly become so small and delicate as to give, at first sight, the appearance of an absence of vascularity in the course of a band of about $\frac{1}{6}$th of an inch in breadth, and extending across a large portion of the free circumference of the capsule.† This is the so-called stigma, at which, when the ovule is to escape from the ovary and to be transferred into the oviduct, the rupture of the theca occurs.

* There may probably be an epithelial lining of this membrane. See H. Meckel's paper, afterwards referred to, Zeitsch. für Wissensch. Zool. vol. iii., 1852, p. 420.

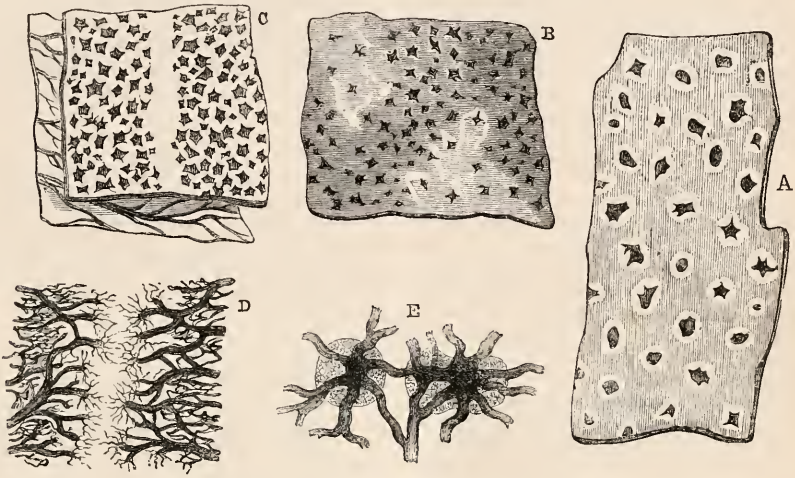
† The length of this band or stigma is about equal to the long diameter, or a third of the circumference of the capsule at its widest part. It is sometimes crossed by a second band of the same kind.

Each developed ovule, therefore, in these oviparous animals, comes to be contained in a pediculated capsule, which is formed by the extension of the substance of the ovary; but from the great extent to which the dilatation of the capsule occurs, the true ovarian stroma is reduced to a very small amount, and scarcely more remaining than the theca of the capsule itself and the ovarian coverings.

In the other animals possessing the large yolked ova, nearly the same structure of the ovary prevails. In chelonia and crocodiles, it is indeed almost identical with that in birds. In lizards and serpents, the hollow state of the ovary produces some difference in the general form; and in cartilaginous fishes (sharks and rays) other differences in the structure of the ovary may exist; but in all these animals the essential points of relation between the ovarian substance and capsules, and the large ovules, are the same as that now described in birds.

The lining membrane of the ovicapsule of birds is thick and tough, and on its inner sur-

Fig. 43.



Structure of the ovisac in the Fowl's ovary.

A. Inner surface of a portion of the ovisac of a fully-developed ovarian capsule, magnified about six diameters, showing an appearance which might be mistaken for glandular depressions produced by the peculiar disposition of the veins.

B. The same, from a calyx from which the ovum has been discharged some days before; a whitish flaky membrane is deposited on portions of the surface.

C. The same, from an undeveloped capsule of a quarter of an inch in diameter, across the stigmatic band.

D. The disposition of the blood-vessels near the stigmatic band, which seems at first sight non-vascular, but is in reality traversed by ramifying small vessels proceeding from the neighbouring larger veins, and crossing the stigmatic band.

E. Two of the large mouths of the veins, which give the semblance of follicular pits represented in A and C, but which are quite closed, with the smaller vessels ending in them, as seen from the inner surface of the ovisac.

face presents a soft appearance somewhat similar to that of a mucous membrane. In examining the inner surface of this membrane, Dr. Sharpey and the author had their attention arrested by an appearance such as might, on first sight, be attributed to a number of follicular or glandular pits. This appearance, as we first observed it, is represented in *fig.* 43. (A, B, C) as it was seen in a fully-developed capsule—in one a third of an inch in diameter—and in a calyx from which the yolk had been discharged some days previously. We supposed, indeed, at first that the appearance depended on the presence of the orifices of follicular depressions or glands on the inner surface of the membrane. A more attentive examination of this membrane by Dr. Sharpey has shown that the appearance is not due to depressions of the inner surface of the membrane or to the mouths of follicles opening upon it, but is caused by a peculiar form of the blood-vessels seen through the entire and smooth inner surface of the membrane. The apparent depressions are in fact the sudden terminations or beginnings of veins of considerable size seen through a delicate and transparent portion of the membrane which closes them towards the inner surface. They may be made very obvious by merely coarsely brushing the smooth blunt edge of any instrument over the membrane, and thus causing the blood to flow from the vessels in other parts in these sinuses or dilated veins.

It would appear that the smaller capillary vessels in which the arteries terminate, in approaching the inner surface of the capsule, ramify with considerable minuteness, and at each of the marks or apparent depressions referred to suddenly fall into or end in the comparatively large veins which constitute the hollow spaces. The ends of these veins, then, look towards the inner surface of the membrane; and the appearance of a divided cavity in some of the supposed follicles is merely caused by two or more veins meeting in a common dilatation at this place. The capillary vessels, in passing into these large commencements of the veins seem to converge from its circumference to its centre.

In the enlarged ovarian capsules of the turtle, a somewhat similar arrangement may be observed; but I have not had an opportunity of tracing its relation to the blood-vessels; nor have I had the means of ascertaining whether anything of the same kind exists in other reptiles with large yolks. In the skate I have not been able to perceive any similar arrangement; and in the Graafian vesicle of mammalia the lining membrane presents internally a smooth surface destitute of any appearance of depressions or of peculiar venous sinuses.

The appearance which I have just now described had not escaped the notice of Von Baer; for at p. 23 of his work on development, he mentions the existence of clearer points in the inner membrane of the theca, and states his opinion that they may be open mouths of blood-vessels, by means of which the yolk may be nourished by the direct access of blood to it.

In the naked amphibia and osseous fishes, the ovaries (of which the general form has been previously noticed) present a still greater decrease in the proportion of the stroma to the ovicapsules and ova. These capsules are themselves also of much more delicate structure than in the higher animals; but the relation of the ovules to the ovicapsules in their formation, and the mode of their escape by the rupture of the theca, are essentially analogous to those of birds and reptiles. In the earliest condition, it is true, the ovary may present a greater amount of solidity in some of these animals; but from the prodigious number of the germs of the ovules and the small quantity of the ovarian stroma, as soon as the ovary has made some progress in development, it acquires the appearance rather of a mere mass of ova connected together by a membrane and fine thread-like pedicles, than of a solid or consistent organ containing them. The delicate ovicapsules containing the ovules embrace them closely as in the large-yolked group of animals, there being little or no fluid between the capsules and the vitelline membrane.

The structure of the ovaries in the invertebrate animals presents so many varieties that it would occupy too much space to allude to them here. I refer the reader for information regarding them to the article ORGANS OF GENERATION, and others on particular classes and orders of animals in different parts of this work. For our present purpose the structure of these organs has been sufficiently indicated in the previous section.

In conclusion, it may be right to recapitulate the general nature of the ovary or formative organ in its relation to the production of ova. A comparison of the forms previously indicated leads to the general view that the ovary is to be regarded as analogous to the glandular organs. In the great majority of animals highest in the scale, the ovisacs are close follicles from which the product of formation (or secretion) escapes by the bursting of the wall of the follicle — in the highest animals, on the external surface of the organ, in those coming next in the series, towards an internal cavity. In other instances, principally among the lower animals, the structure is more analogous to that we are accustomed to consider as characteristic of the true glands, in which the secreted cellular product is formed within the same or a continuation of the tubular ducts themselves by which they make their escape. The more complex structure of the capsules in which the large-yolked ovules are produced in birds constitutes a special apparatus, which, though without follicular complication, may be looked upon as a modification or higher degree of development of the glandular structure of the ovary, provided for the rapid formation of the larger mass of nutritive substance which is present in these ova.

§ 4. *More detailed description of the ovum of birds as the type of the* 1*st group.*

Having in the previous section given a sketch of the general resemblances and differences observed among the ova of various animals, I now proceed to describe more in detail an example from each of the three groups previously distinguished, and more particularly those of Birds and Mammalia, which demand the greatest share of our attention in the study of development; and first as to the ovum of the common fowl.

Quantity of matter, composition, &c. — The average dimensions of the fowl's egg in this country are the following: The long diameter 2¼ inches, short diameter 1¾ inch. The average weight of eggs of this size is a little more than 2 oz. avoird., or 920 grains.*

The extremes in weight which I have observed among eggs of the fowl naturally formed are 750 and 1060 grains. Double-yolked eggs are, as might be expected, much larger, reaching often a weight of 1400 grains, or 3¼ oz.

The yolk weighs about a third of the whole; the albumen, membrane, and shell forming the remaining two thirds. These parts of the egg are in the following proportions to each other in 100 parts; the albu-

* The following is a comparative view of the average size and weight of the eggs of the common fowl, duck, turkey, and goose.

	Length (in inches).	Breadth (in inches).	Weight (in grains).	
Fowl -	2·25	1·7	920 nearly	2 oz.
Duck -	2·5	1·75	1100	2½ oz.
Turkey	2·7	1·9	1300	3 oz.
Goose -	3·3	2·4	2600	6 oz.

men 58, the yolk $31\frac{1}{2}$, and the shell with its lining membrane, $10\frac{1}{2}$.

When eggs are kept exposed, they gradually sustain a small loss, due chiefly to the evaporation of water, and amounting to about one grain per day. When putrefaction ensues, an additional loss from chemical changes occurs.

During incubation, the loss of weight is more considerable, amounting in twenty-one days to 16 or 17 per cent., or nearly one sixth of their entire substance.* The loss by an egg during incubation, therefore, is eight times as great as that which occurs in an egg kept at the usual atmospheric temperature for the same period — a circumstance which depends partly on the higher temperature, but principally on the evolution of carbon from the oily matters of the incubated egg, in combination with the oxygen of the air, or as carbonic acid, &c.

Of the 17 parts per cent. lost during incubation, not more than $5\frac{1}{2}$ or 6 consist of water, and the remaining two thirds, that is 10 or 11 parts, are derived from the oily and other substances of the egg which undergo chemical changes attendant upon the process of organisation and respiration of the embryo.

By evaporation to dryness of the whole egg without the shell and membrane, about 27 per cent. of the substance are left; the oily ingredients of this residue, amounting to about $10\frac{3}{4}$, are almost all contained in the yolk, and the remaining $16\frac{1}{4}$ parts of solid matter are nearly equally divided between the yolk and the white. The yolk, therefore, is much richer in the fixed and solid parts than the white; but its specific gravity, as will afterwards be seen, is considerably reduced by the larger quantity of oily matter it contains: the per-centage of solid matter (independently of the oleaginous substance) contained in the yolk and albumen, is in the proportion of 32 in the first to 14 in the second.†

The solid residue obtained by evaporation of the white at a low temperature, amounting to nearly one seventh of the whole, consists chiefly of albumen; along with which there is also some animal matter which has hitherto been named by chemists as extractive, and a small amount of salts, which are principally alkaline sulphates, muriates and phosphates, with phosphate of lime, some free soda and sulphur.

The yolk contains little more than half its weight of water, or 54 per cent. The remaining 46 parts consist of about 17 of albumen, or analogous principles, 28 of oily matter, and $1\frac{1}{4}$ of salts. These last are chiefly alkaline muriates and sulphates, phosphate of lime and magnesia, and traces of iron, sulphur, and phosphorus. The albumen has an alkaline, the yolk a neutral, reaction.*

The membrane lining the shell consists apparently of a protein compound, analogous somewhat to that of the elastic yellow tissue.

The shell consists of earthy salts deposited in a delicate matrix of animal matter, which last constitutes not more than 3 per cent. of the whole. The earthy ingredients are in great part carbonate of lime, together with a little carbonate of magnesia, and phosphate of lime and magnesia.

Of the ingredients of the egg before mentioned, the albumen and other animal principles, together with the sulphur and salts, are no doubt more immediately employed in the growth of the embryo; while the oily matter, besides contributing, as it appears, in some part, to the same purpose, serves more directly and in greater quantity for the respiratory process, in which it is consumed largely during incubation.

The alkalinity of the white of egg appears to depend on the presence of caustic soda, which albumen has the property of separating from its carbonate.

The following tabular view exhibits in a general way the change in the relative proportion of the ingredients of the egg resulting from incubation†: —

	Fresh egg.	Incubated egg.
Shell and membrane - -	10·67	10·
Albumen, &c. - - - -	17·8	19·4
Oily matter, &c. - - -	18·83	6·5
Water - - - - - -	52·7	47·1
Loss { Water - 5·6; Oily matt., &c. 11·4 }		17·
	100·00	100·00

When an egg is examined immediately on being laid and while yet warm, or still better when taken from the egg-bag of the fowl previous to laying, the yolk and white fill completely the interior; but immediately on cooling, a small space or vacuity appears generally towards the obtuse end of the egg, and this air-space increases gradually in size as the eggs are longer kept and the natural evaporation of water proceeds. This space is formed by the separation of the two principal layers of the lining membrane of the shell. During incubation the air-space increases much more rapidly; and indeed towards the end of this

* See Prout, On the fixed Principles of the Egg, Philos. Trans. and Annals of Philos. for 1822. Also, by the same author, On the Changes of the Egg in Incubation, in the same Journal, for 1823.; and, Paris, On the Physiology of the Egg, in Linnean Soc. Trans. vol. x. p. 304, and Annals of Philos. 1821.

† See Prevost and Morin, in Journ. de Pharmacie for 1846, and Sacc, in the Eggs of the Bantam Fowl, in Annal. des Scien. Nat. for 1847, p. 69.

* Composition of the yolk, according to Gobley, in Journal de Pharmacie, 8e. sér. tom. ix. p. 174.

Water, about - - - -	53·
Vitelline, albumen, and protein compounds - - - - -	16·5
Oily matters - - - - -	29·
Salts, &c. - - - - -	1·5
	100·0

These salts are the following — viz., chloride of sodium and potassium, sulphate of potassa, muriate of ammonia, phosphates of lime and magnesia, lactic acid, colouring matter, iron.

† From Sacc, loc. citat.

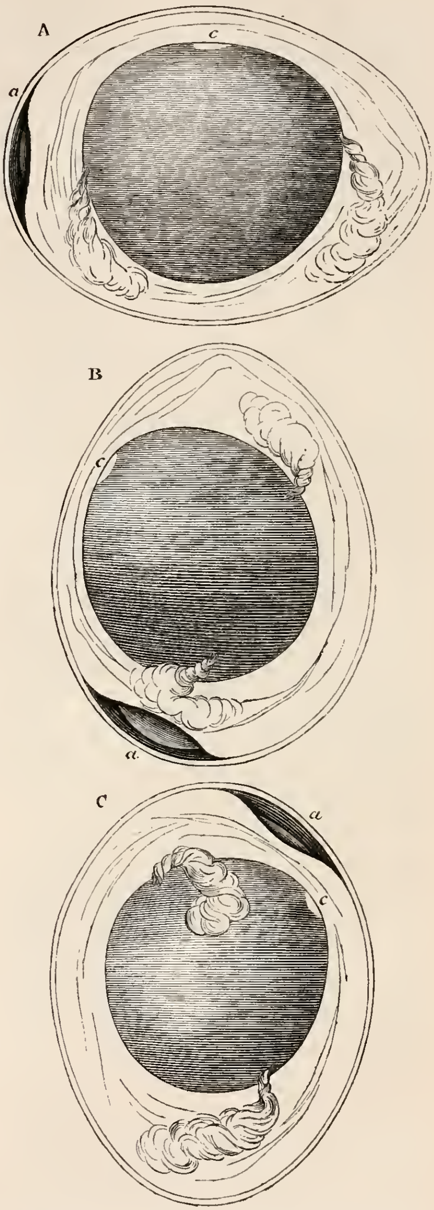
process, and in eggs that have been long kept, the space has extended over the whole width of the egg, and the quantity of gas contained in this space is sufficient to cause the eggs to float in water. The extent of the air-space may be ascertained in some degree by the greater or less feeling of coldness of the shell of the egg near the obtuse end, when it is applied to the skin of a delicate part, such as the eyelid, in consequence of the heat being less rapidly carried off by that part of the shell within which the air-space has been formed, than at others with which the albumen is in contact.

Dr. Paris found this air, amounting to about half a cubic inch, to be nearly pure atmospheric air, with a small quantity of carbonic acid towards the end of the period of incubation. MM. Baudrimont and St. Ange find it to contain in general more oxygen than atmospheric air, and no carbonic acid; whence they conclude that the shell has a peculiar power of passing outwards the carbonic acid formed during incubation and taking in oxygen.* The formation of the air-space is manifestly a compensation for the loss of substance in whatever way occasioned, that may take place from the egg. We shall have occasion afterwards to consider in how far it may be important in connection with the phenomena of incubation.

The specific gravity of the whole egg, when newly laid, and before evaporation has taken place, is generally as high as 1090, being raised considerably above the common specific gravity of the fluids and soft parts of animals by the superior density of the shell; but as the air space increases, the whole specific gravity will be lowered.

The specific gravity of the albumen and yolk differ in a considerable degree; that of the yolk, though containing the largest amount of solid matter, being lowest in consequence of the large quantity of oily matter belonging to it; and thus when the albumen becomes more fluid during incubation, the yolk naturally rises towards its upper part, or displaces some of the albumen which lay above it in the newly laid egg. It is also an interesting circumstance, that the specific gravity of the lower and upper parts of the yolk differs perceptibly; that of the upper part being reduced by the greater quantity of oily matter contained in the cells situated in the vicinity of the cicatricula. The upturning of the side of the yolk bearing the cicatricula, which is familiarly known, has long excited attention; and several explanations have been suggested of its cause; and, among others, the chalazæ have been supposed to balance the yolk in such a manner as to secure this position. But Von Baer showed that this view was erroneous, and that the less specific gravity of the upper part, or of that portion of the yolk in which the cicatricula is placed, is the true cause of the phenomenon. The measurements of the specific gravity of different parts of the egg by Messrs.

Fig. 44.



Position, form, and attachment of the chalazæ, yolk, and cicatricula, as shown by sections of fowls' eggs boiled in different positions.

A. Section of an egg, boiled on its side: B, with the narrow end up: C, with the wide end up These figures show the tendency of the lighter part of the yolk, on the surface of which the cicatricula, *c*, is situated, to be buoyed up and to expand in the white, at the same time that the movements of the yolk are to a certain extent limited by the attachment of the chalazæ; *a*, air-space.

* Recherches Anat. et Physiol. sur l'Œuf des Vertebrés, Mém. Couronn.; published in Mém. des Savans Etrangers de l'Acad. Fran. 1850.

Baudrimont and St. Ange* are quite confirmatory of this view. They are as follows: —

Sp. gr. of the	External albumen	1041·
„	Internal albumen	1042·5
„	Whole yolk	1029·5
„	Upper part of yolk	1027·
„	Lower part of yolk	1031·5†

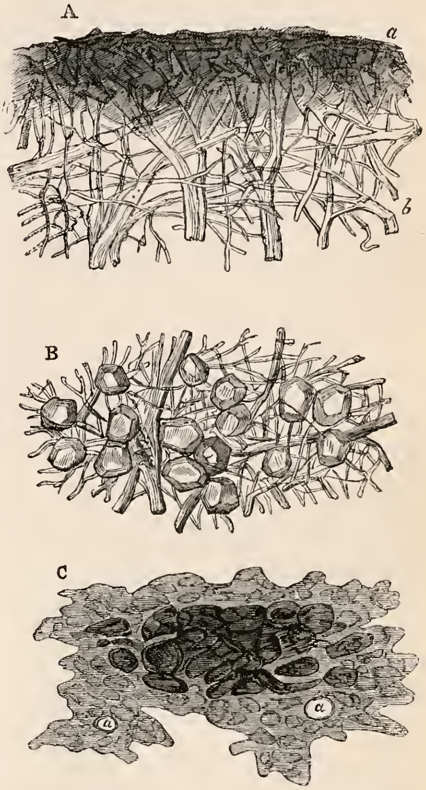
The chalazæ, being of greater specific gravity than even the inner layer of white, always float lowest; but, being attached to the yolk near its poles, they hang down from these points. All these circumstances may be illustrated very clearly by sections of eggs that have been boiled in different fixed positions, as on the side, on the large and small end; in which it will be found that, while the chalazæ exercise a certain control over the position of the yolk, that portion of its surface containing the cicatricula rises higher and expands more fully within the white than the opposite portion, while the chalazæ gravitate towards the lower side. (*See fig.* 44.)

Structure of the external parts of the egg.— The shell of the bird's egg is composed of a delicate basis of organised animal matter impregnated with the calcareous and earthy particles, the arrangement of which approaches to a crystalline appearance, but is probably of a different nature. This substance is porous, like concreted gypsum-plaster, and allows of evaporation and the mutual diffusion of gases through it in the same manner as that substance; while, by its strength and rigidity, it affords protection and support to the softer parts of the egg during incubation. The pores of the egg-shell may be easily stopped by any greasy or oily matter, or by melted wax or varnish; and then all passage of moisture or air through the shell being prevented, the development of the embryo becomes impossible. Eggs that have been oiled cannot, it is well known, be hatched; but eggs may be kept for a considerable time — weeks, or even for months — by immersion in lime-water, which impedes the evaporation and the access of air, which might favour putrefaction, while the natural condition of the contents is thus preserved.

The shell in most eggs is slightly dimpled externally, with small depressions visible to the naked eye; but these are not the openings of the pores through which evaporation or exchange of gases takes place — these being much more minute and numerous—but merely the indication of depressions caused by the largely villous structure of that part of the oviduct (uterus) in which the calcareous shell is deposited.

On removing the earthy matter by means of a dilute acid, the animal basis remains as a slightly coherent, cellular, organised structure, the form of the small compartments in which corresponds with that of the calcareous particles of the shell (see *fig.* 45. c). The in-

Fig. 45.



Structure of the shell and shell-membrane in the Fowl's egg.

A. Lining membrane of the shell; *a*, thick matted or felty portion; *b*, thin shred of the torn margin, showing the peculiar fibrous tissue of which the various layers are composed.

B. Outermost layer of the same, which is incorporated with the shell; some of the angular corpuscles of the shell lying upon the fibrous substance and firmly united with it.

C. Small portion of the calcareous shell, which has been steeped in dilute hydrochloric acid, showing the remains of opaque calcareous substance in the centre, some portions of it exhibiting a granular aspect, and round the margins the animal basis or matrix from which the calcareous matter has been dissolved, presenting an irregular granular or almost amorphous aspect. Here and there clear oval cells are seen, as at *a a*.

ternal surface is irregular and flocculent, and adheres very closely to a different kind of membrane which lines the shell.

In those instances in which the shell of eggs is coloured, the pigment substance, of various hues, is generally deposited in cells, which are strewed uniformly or in patches over the external surface of the calcareous shell. In some other instances, however, the

* Op. cit.

† Dr. Wm. Aitken has, at my request, repeated these experiments, and has obtained results in accordance with the above statement. He found the unboiled yolk to float indifferently in any part of a saline fluid of specific gravity 1035. By boiling, the specific gravity was reduced to 1031, and in both cases the side with the cicatricula floated uppermost. The upper half, containing the cicatricula, had a specific gravity of 1030; the lower half, 1032.

colour seems to be merely a uniform tinge of the outermost layer of calcareous matter.*

The lining membrane of the shell is a peculiar fibrous, interwoven structure, deposited in laminæ of some thickness and toughness, which is readily divided by tearing into two layers over the whole surface of the egg — an outer, thicker, and denser, adhering firmly to the inner surface of the shell; and an inner, thinner, smoother, and of finer texture, which may be easily withdrawn from the outer one, and which naturally separates from it at the air-space; but both the outer and inner layers of this membrane may be torn into a number of thinner laminæ, all agreeing in their minute structure.

By microscopic examination, this membrane is found to consist of a closely-interwoven network of peculiar fibres, which are of various sizes, generally between $\frac{1}{8000}$th and $\frac{1}{3000}$th of an inch in diameter; the larger frequently branching into or giving off smaller fibres at acute angles, the sides rendered uneven by minute projections or knots upon them (not represented in the figure); the larger fibres are of a somewhat flattened or ribband-like form. The external layer of the membrane contains the largest fibres. These fibres appear to be analogous in their chemical nature to those of the elastic yellow texture, not being soluble in strong acetic acid; but they do not coil up in the manner of the elastic tissue (see *fig.* 45. A).

The parchment-like coverings of the eggs of serpents and lizards, which have no calcareous shell, seem to be composed of a greater number of layers of the fibro-laminar texture now described.

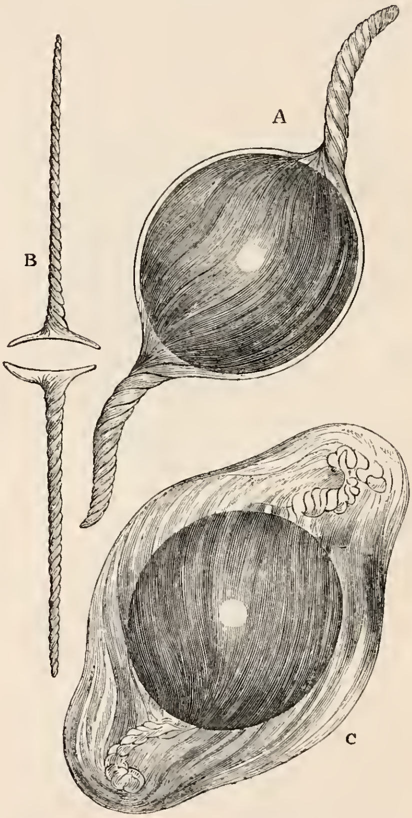
The albumen, or white of the egg, comprehends several layers of glairy, albuminous, semifluid substance deposited round the yolk, the chalazæ, or grandines, or twisted cords, and the condensed layer of albumen, forming a thin membranous investment immediately over the yolk membrane. In a perfectly-fresh egg, or in an egg taken from the oviduct previously to its being laid, the whole albumen has the consistence of a moderately-firm jelly; but very soon the outer part becomes fluid, and allows of the freer motion of the parts within the shell. This solution of the albumen proceeds to a greater extent after some hours' incubation, especially over the cicatricula.

The deeper part of the albumen, or that next the yolk, is more dense in consistence. No part of it, when unchanged by reagents, presents any sensible structure either to the naked eye or when viewed microscopically. If, however, the soft contents of a fresh egg, or one removed from the oviduct, be taken from within the shell, and thrown into water either pure or with a little acetic acid mixed with it, a slight turbidity or coagulation of the albumen takes place on the surface, which brings out the appearance of a spiral arrangement of laminæ; and in a boiled egg these laminæ may be torn in great numbers in succession from off it, the direction of the spiral being from left to right, from the large towards the small end of the egg. With a little care, almost the whole of the albumen may thus be wound off the egg in spiral strips, the deeper ones enclosing the twisted chalazæ (see *fig.* 46. D).

The coagulated albumen presents, in the microscope, a minute but indefinite granular structure.

The *chalazæ* (*grandines*) are two irregularly-twisted cords of albumen, harder than the rest,

Fig. 46.



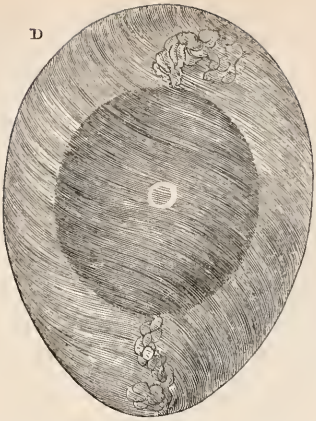
Manner in which the chalazæ, albumen, &c., are deposited round the ovarian ovum of the Fowl.

A. Yolk from the upper part of the oviduct soon after it has entered it, showing a thin covering of albumen on the yolk, forming the chalaziferous membrane, and the twisted chalazæ extending from the opposite poles of the yolk The twisting in these is represented more strongly than it can be seen at this period.

B. Sketch of the fully formed chalazæ from opposite sides of the yolk, stretched to their full length, and showing the opposite direction of the spiral in each.

C. Egg from above the middle of the oviduct; the first layers of albumen deposited round the yolk and chalazæ.

* See the works of Hewetson and others on the Eggs of Birds. Carus and Otto, Erlauterungstafeln der Vergleich. Anat. part v.



D. Egg from the lower part of the glandular oviduct near the isthmus, when the deposit of albumen is complete; the spiral arrangement of the albumen made manifest by slight coagulation.

attached to the opposite ends or poles of the yolk by means of a membrane which looks exactly like a continuation of the twisted part of these bodies opening or expanded over the surface of the vitelline membrane. These bodies attracted considerable notice from the earlier observers of the structure of the egg, and have had various uses attributed to them; but, if we may judge from the varieties they are subject to in the fowl and other birds, and their absence in the ova of scaly reptiles (otherwise very similar to those of birds), it would appear that they are only of secondary importance.

One of the chalazæ is directed towards the larger, and the other to the smaller end of the egg, and the latter usually adheres with some firmness to the inside of the shell-membrane, while that of the large end floats more freely. In this manner the yolk moves more freely at the large than at the small end of the egg. The spiral twist is in opposite directions in the two chalazæ; a circumstance depending on the manner of their production, by the gradual deposit of albumen and the spiral motion of the yolk during its descent in the oviduct. The membrane which proceeds from the chalazæ over the surface of the yolk has been called chalaziferous; and the funnel-shaped dilatation of the chalazæ where they join the membrane, has been supposed to be the opening of a tube passing through these bodies, and serving as a conduit from the white to the yolk; but entirely without reason. The chalaziferous membrane and innermost twisted part of the chalazæ are, in fact, nothing more than the first-deposited and densest parts of the albumen; nor is any importance to be attributed to a curved line or fold of the membrane which is often seen stretching over the yolk between the adhering parts of the opposite chalazæ.

The fact of the upturning of the side of the yolk which bears the cicatricula has already been adverted to, as well as the supposition that the chalazæ may be the means of securing this position; but, although it is well ascertained that these bodies control, in various directions, the motions of the yolk, they cannot be the cause of the upturning of the cicatricula; as this is secured by the difference of specific gravity in the upper and lower parts of the yolk. The true action of the chalazæ is to limit the motions of the yolk in the long axis of the egg, and control the rotation during a certain time; but in incubation the relations of the chalazæ, white, and yolk are very soon changed; and, in the progress of these changes, the remains of the denser white are collected at the lower part of the egg. If a fresh egg be turned round on its long axis, the cicatricula will keep its position upwards for one turn or a little more, and then, by the twisting of the chalazæ, the yolk is carried completely round, and balances itself again with the cicatricula uppermost in its new position.

The accessory parts of the egg, now described, are formed round the yolk or ovarian egg during its descent through the oviduct; and as they may be regarded as only indirectly connected with the functions of the true ovulum in their relation to embryonic development, it may be best to complete their history at this place by stating what has been observed as to their formation, referring for this to the researches of Purkinje, Coste, and others, which I have confirmed in most particulars by the examination of a considerable number of fowls during the process.

Formation of the external or accessory parts of the bird's egg.—These parts are produced with much greater rapidity than those of the ovulum. Many fowls lay an egg every twenty-four hours for a part of the season, while others lay only every second day, or two or three days in succession, generally at a later hour on each successive day, and then intermit for a day; other fowls lay regularly nearly every thirty-six hours. There is probably some difference in the rapidity of the descent of the egg, or at least in the length of time it remains in particular parts of the oviduct, in these various cases; but in general the whole passage of the egg, from the time of the reception of the yolk by the infundibulum to its being laid, occupies about twenty-four hours.

If a fowl which is laying only every second day, be killed and opened from seventeen to twenty hours, or if one which is laying daily be opened from three to six hours after the last egg was deposited, one of the ovarian capsules will sometimes be found completely enveloped by the infundibulum of the oviduct, which is thus in the act of receiving the ovulum or yolk about to be discharged by the cleaving of the capsule along the stigmatic band.* The infundibulum is contracted round the neck or pedicle of the ovarian capsule, so that the whole is embraced by it with moderate firmness, and the yolk thus usually passes securely into the

* See a later section for an account of the circumstances which influence the discharge of the ovarian ovula.

oviduct; but it occasionally happens that capsules burst without being so embraced, or that the process is disturbed, and the substance of the yolk falling into the abdominal cavity of the fowl either produces serious injury by peritoneal inflammation, or may be gradually removed by absorption.

The yolk enters the infundibulum, with its long axis corresponding to that of the oviduct, consequently with the cicatricula on its side, which we shall find to be its position also in the completed egg.

The passage of the yolk through the first two-thirds of the length of the oviduct, in which part the albumen is deposited, is very rapid, scarcely occupying more than three hours, according to Coste*, before it arrives in the narrow or constricted part of a more limited extent (isthmus), in which the membrane of the shell is formed. About three hours more suffice for this process, and the ovum then enters the dilated portion, which has been called uterus, in which the substance of the shell is deposited and gradually consolidated on its surface.

The albumen begins to be deposited round the yolk, immediately upon the entrance of the latter into the oviduct; at first in a thin layer, immediately investing the yolk, which subsequently becomes condensed into the chalaziferous membrane, and in two long narrow portions extending before and behind the yolk from its poles, which portions of albumen are at first straight and simple, but afterwards become twisted and form the chalazæ. (See *fig.* 46, A.)

In the next part of the albuminiferous part of the oviduct, in which the glandular structure is most fully developed, the albumen is deposited in much greater quantity round the yolk and chalazæ, not following the form of the latter, and thus soon gives to the whole the oval shape which belongs to the egg; and we then recognise, previous to the formation of the shell or its lining membrane, that the narrower end of the oval is placed downwards, or advances first in the oviduct.

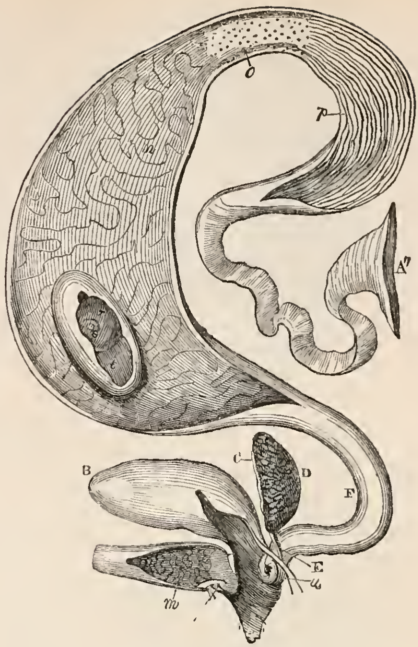
During the passage of the egg, and the formation of the albumen, membrane, and shell, a greatly increased determination of blood is observed in the vessels of the several parts of the oviduct. (See *fig.* 47.)

The formation of the accessory parts of the egg appears to proceed nearly in the same manner in the scaly reptiles as in birds. The accompanying figure, borrowed from the article Reptilia, is illustrative of the main features of the process.

The advancing motion of the egg of the fowl is caused by the peristaltic action of the muscular coat of the oviduct, which may be easily seen in any laying fowl opened immediately after death. The egg does not descend, however, in a straight line, but in a spiral direction, corresponding with that of the ridges of glands with which the mucous membrane of the oviduct is beset. Two peculiarities in the structure of the albuminous part of the egg result from this spiral motion—viz.,

* Hist. gén. et partic. du Dével. &c.

Fig. 47.



Descent of the egg in the oviduct of the Tortoise (after Bojanus).

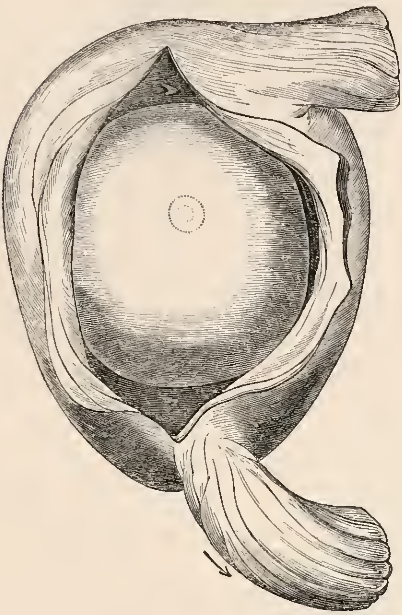
A. Infundibular opening of the oviduct; *n, o, p*, canal of the oviduct laid open; *s, t*, ovum opened, showing the yolk, albumen and shell; B, allantoid bladder; F, oviduct; C, D, kidney; E, ureter; *m*, termination of the opposite oviduct.

the spiral laminated form of the outer layers of albumen, and the marked tortuosity of the chalazæ. It is easy to understand how the spiral form is given to the deposit of the layers of albumen. The cause of the peculiar manner in which the chalazæ are twisted is not so immediately apparent ; it may be explained as follows. As already remarked, the spiral twist is in an opposite direction in the two chalazæ; one end of each of these cords must, therefore, have remained in a state of rest as compared with the other. Either, it may be supposed, the farther ends of the two chalazæ extending into the oviduct before and behind the descending yolk, remain comparatively at rest, while that body with the albumen forming round it being closely embraced by the oviduct has the rotary motion impressed upon it; or, as is more probable, when the chalazæ become attached to and involved in the deposited albumen, their outer ends move with it, while the yolk within, to which the inner ends of the chalazæ are fixed, does not rotate in the same degree; a circumstance to which it is possible the disposition of the side on which the cicatricula is placed to remain uppermost may in some degree contribute; and thus the yolk not turning so rapidly, or so often as the white, the chalazæ are twisted upon their roots attached to the surface of the yolk.*

* It ought to be observed, however, that according to Coste, the yolk does not at first rotate freely

Although it can scarcely be doubted that the chalazæ are produced during the descent of the egg, while the albumen is being deposited, it is worthy of remark, that the twisted structure of these bodies is usually not to be seen till after the shell has begun to be formed*; but it is very probable that

Fig. 48.



Position of the egg in the oviduct as it descends.

A portion of the oviduct near the lower end opened, taken from a fowl killed three and a half hours after the last egg was laid. The greater part of the albumen has been deposited, and the egg has assumed its peculiar form, the small end of the oval advancing first; the cicatricula placed on the side of the yolk.

this may depend on their not having previously acquired sufficient opacity or condensation to render their tortuous structure obvious. Indeed, Von Baer has observed them to make their appearance by increase of their opacity from exposure while under actual observation.

It has been ascertained by experimental observation that the membrane of the shell is formed in the narrow part of the oviduct, termed the isthmus, which intervenes between the albuminiferous part and the uterine dilatation. It consists, no doubt, in the fibrillation of consolidated albumen, or some analogous substance, which must take place with great rapidity; but we are not yet sufficiently acquainted with the nature of this process, for the phenomena of the solidification and fibrillar organisation have not been minutely examined, nor has any difference yet been ascertained between the substance secreted in the isthmus, which undergoes the fibrillation without calcification, and that of the uterine dilatation, which seems to have no such tendency, remaining amorphous or cellular, and having very soon a deposit of calcareous matter formed in it.

By the time the egg arrives in the uterus, it has acquired its peculiar oval form, the small end pointing downwards in the oviduct. The cause of this form, which is already apparent in the white previous to the formation of the shell, is somewhat obscure, on account of the complexity of the mechanical conditions influencing the egg in its passage. It may probably depend on the circumstance that the soft mass dilates the oviduct more gradually as it insinuates itself between its coats, in being propelled onwards, while the part of the duct through which it has passed contracts more abruptly and firmly in consequence of the stimulus of distension to which it has been subjected. But the variety of forms which occurs in the eggs of different birds and other animals must not be forgotten, as indicating that the peculiarity of a lesser and greater end is not essential, and may depend on very slight or transient circumstances. Perhaps, the greater density of the albumen, secreted over the end which advances first in the oviduct, may also have some effect in giving this part the smaller volume. It certainly seems remarkable that the ends of the egg should be moulded into so smooth and rounded a surface as that of the membrane and shell by a tubular organ. In some rare instances, however, I have observed irregularities of form at the extremities of the egg, indicating an imperfect contraction of the oviduct during the passage.

The egg remains a much longer time (from twelve to eighteen or more hours) in the uterine dilatation of the oviduct during the formation of the shell. The mucous membrane of this part differs in structure considerably from the rest: it presents over its whole extent large villous-like processes, or short folds, of a flattened form, containing small follicular glands, from which the substance of the shell is secreted. As soon as the egg enters this part of the passage a thickish white fluid is poured out from the membrane, which speedily coagulates on the surface of the membrane lining the shell, and very soon we can perceive with the microscope small heaps or united groups of particles somewhat of a crystalline appearance, but in reality calcified blastema studded over the whole surface. These are the calcareous particles of the shell, which are deposited in a delicate matrix of animal tissue of a large cellular structure. The deposit goes on rapidly increasing: at first the shell is soft, it remains friable for a considerable time, and, subsequently, it

within the white, and that it is only towards the end of the period of its passing through the oviduct that a liquefaction of the albumen, which then occurs, permits this rotation: but I think it doubtful that the adhesion between the surface of the yolk and deeper albumen is so great as to prevent the degree of rotation above referred to.

* Von Baer, Uber Entwick. p. 31.

gradually acquires the peculiar dry hardness which characterises it after the egg is laid.* The view of H. Meckel that the animal basis of the shell is formed by the separation of a layer of the mucous membrane of the uterine part of the oviduct does not appear to be established.

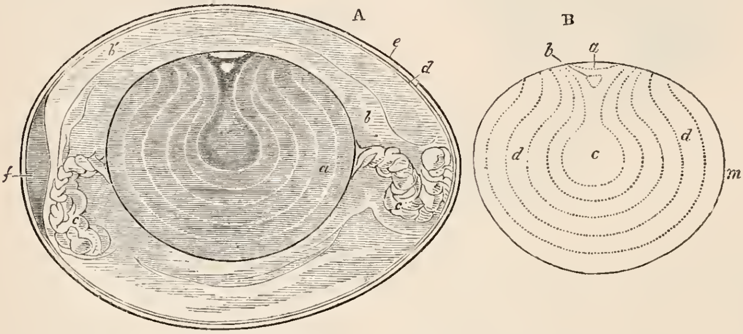
During the time that the shell is forming, the distinction between the softer and thinner external albumen, and the more dense and deeper part, becomes more obvious, and, at the same time, according to M. Coste, a certain degree of liquefaction occurs in a layer of albumen immediately surrounding the yolk, which allows the latter body to float more freely within the superincumbent albumen.

The egg remains in the uterine dilatation till it is about to be laid. The expulsion of it from this cavity through the narrow part of the tube, leading into the cloaca, requires very strong muscular contraction for its accomplishment; and, although the egg always descends in the oviduct, and usually lies in the uterus, with its narrow end downwards, both Purkinje and Von Baer state that they have sometimes seen its position inverted towards the end of the time of its residence there in consequence of the force of the muscular contractions of the wall of the oviduct.

Ovarian ovum of birds; ovulum; yolk and its contents.—The yolk, yelk, or vitellus (*Jaune*, Fr. *Dotter*, Germ.) consists in the newly laid egg of the external enclosing vitelline membrane, of the yolk substance, a mass of vesicular, cellular, and granular matter of various structure, to which as a whole the membrane gives a subglobular form, and on the surface of this mass, below or within the vitelline membrane, and on that side of the yolk which naturally turns uppermost in the complete egg, the cicatricula, or embryo spot, a thin disc of organised cellular structure, in which, under the influence of heat and air, as during ordinary incubation, the embryo, and its accompanying fœtal membranes, &c., are first formed.

The cicatricula of the laid egg, as has already been remarked, however, has, during its descent through the oviduct, undergone some part of those changes which belong to the

Fig. 49.



Form of the Fowl's egg and structure of the yolk as exhibited by a section.

A. Sectional view of the fowl's egg; *a*, yolk enclosed by its vitelline membrane; *b*, *b'*, inner and outer parts of the albumen: *c*, *c*, chalazæ; *d*, two principal layers of the lining membrane of the shell; *e*, calcareous shell; *f*, air-space between the two layers of the shell membrane.

B. Outline of the yolk; *a*, cicatricula; *b*, nucleus of the cicatricula; *c*, yolk cavity or latebra, and canal; *d*, concentric deposits of yolk substance or halones; *m*, vitelline membrane.

fecundated condition, and by which the foundation is laid of that structure in which the future embryo is more immediately developed; for it has now lost its germinal vesicle, and from being formed, as at first, of mere granules or simple spherules, it has acquired a true organised cellular structure. It now consists, in fact, of the delicate discoid collection of cells, which has been called *blastoderma*. It may be proper, therefore, to consider the mass of the yolk and the germ, in their unfecundated state, while still within the ovarian capsule, next, after the ovulum has entered the oviduct, and, subsequently, when it is laid; reserving, however, for a latter part of the article the account of the process by which the change in the cicatricula referred to takes place.

In the newly laid egg the yolk forms an ellipsoidal mass, somewhat flattened on the upper or cicatricular surface, and with its long axis corresponding to that of the egg. Its largest diameter is about one inch and a quarter, its shortest about an inch: it floats within the white, capable of a certain degree of motion, which is controlled, as before explained, by its own specific gravity, and by the attachment of the chalazæ.

The yolk substance is not of the same nature throughout, there being a part of a lighter colour in the centre, about one fourth of the diameter of the whole; from this, a narrower prolongation extends upwards

* It is to be remarked that the animal basis of the calcareous shell is of quite a different structure from the fibrous lining membrane of the shell; and the calcareous deposit is not to be regarded as taking place in that fibrous membrane. The outermost layer of the lining membrane adheres very firmly to the shell, which may have misled some on this point, who describe the animal basis of the calcareous shell as of the same structure with the fibrous lining membrane.

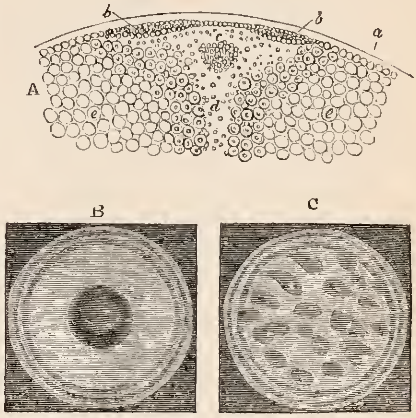
towards the cicatricula, near which it again widens and spreads out like a shallow cone. This whiter internal substance constitutes what has been called the central cavity (or latebra) of the yolk: the whole of this inner part has something of the shape of a flask, with a narrowing neck and a wider mouth at the top, which is, as it were, surmounted or closed in by the cicatricula. (See *fig.* 49.)

The shape of the yolk, I have said, is not that of a regular ellipsoid; the less density of the upper part, which is towards the cicatricula, giving rise to a widening of the yolk on that side, as may be seen in *fig.* 44, A, which represents a vertical section of an egg boiled while lying on its side. This does not depend simply on the rising of oil globules in greater quantity to the upper side of the yolk, but, as has already been noticed, on the fixed predominance of globules containing oil in the neighbourhood of the cicatricula.

Neither is the outer deeper-coloured portion of the yolk altogether uniform in structure or appearance; for it will be seen, both in the raw and boiled egg, but most easily in the latter, that several concentric layers surround the central cavity and canal of the yolk, as well as the funnel-shaped dilatation which lies below the cicatricula. These layers are marked by a slight variation in colour, and are attended by a difference in the minute structure of the corpuscles composing the alternate layers. They probably depend upon the growth of the coloured part of the yolk being more or less rapid at different successive periods.

The cicatricula of the newly laid egg is a spot of an opaque yellowish white, easily distinguished by its difference of colour from the rest of the yolk, about one sixth of an inch in diameter, and lying immediately within the vitelline membrane, in connection at its margins with the most superficial layer of the yolk substance. Examined in a favourable light* it will be found, that in the laid egg, when fecundated, the cicatricula consists of a central clearer and thinner part, and of an external more opaque annular portion. The central part is about one third the diameter of the whole, and seems as if it perforated the remainder of the disc with a circular aperture, something after the manner of the pupil of the iris. There is not, however, any perforation in reality, but only a greater thinness and transparency of the central part of the disc. Neither is this central part entirely clear; for there is placed below its middle a round heap of whitish granules, described by Pander as the *nucleus cicatriculæ* (see the figure in section), which gives greater opacity to that part when viewed directly from above. The central part of the cicatricula, already obvious when the egg is first laid, is the same which, after some hours of incubation, expands, changes its figure, and becoming still

Fig. 50.



Structure of the cicatricula in a laid Fowl's egg.

A. Diagrammatic section of the yolk near the cicatricula, enlarged; *a*, vitelline membrane; *b*, cicatricula; *c*, nucleus; *d*, canal leading to the cavity; *e*, *e*, large yolk corpuscles of the coloured part: the corpuscles are not represented of their real proportional sizes, but more with a view to show their general difference.

B. Enlarged view of the cicatricula, as seen from above on the surface of the yolk in an impregnated egg: the dark central space or transparent area surrounded by an opaque zone and one or two delicate haloes.

C. Cicatricula of an unfecundated laid egg: instead of the central transparent area a number of rather irregular transparent spots are seen.

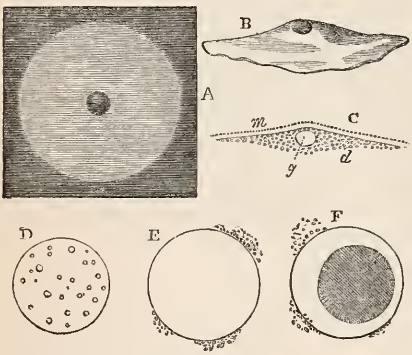
more clear, receives the name of transparent area, in the centre of which the embryo begins to be formed; while the outer more opaque part retains its greater thickness, and is converted afterwards into the vascular and peripheral part of the germinal membrane which spreads over the yolk. Round the margin of the cicatricula the deeper-coloured yolk substance is seen even in a perfectly fresh or newly laid egg to be intersected by one or more fine circles of a lighter colour. These seem to be the same which afterwards, expanding and widening, constitute the *haloes* which precede and accompany the extension of the germinal membrane over the yolk. These circles are the terminations at the surface of the concentric layers of lighter substance, which, as already mentioned, may be seen surrounding the central cavity and canal of the yolk (see *fig.* 49). It seems not improbable that, the difference in the structure of the central and peripheral parts of the cicatricula just stated proceeds from, or is connected with, the peculiar process of fissuring or segmentation which follows the disappearance of the germinal vesicle from its central part in the fecundated egg; but the description of this process belongs to a later section of the present chapter.

* It may be here mentioned, that by far the best mode of examining the natural appearances of the parts as they lie in the opened egg, is to allow a ray of strong or of direct sunlight to fall upon the part which it is wished to investigate, through an aperture in a screen, which places the rest of the egg and the observer in comparative darkness.

The cicatricula of the unfecundated egg, such as is laid by fowls secluded from the cock, differs from that now described principally in the absence of the marked distinction between the central clear and the peripheral opaque part. The germinal vesicle, which to all appearance remains the same in the ovary till the yolk leaves the ovarian capsule, is now no longer to be seen; and the cicatricula is often marked irregularly throughout, but more especially towards the circumference, with clearer intervals, or small irregular circular or oval spaces, mingled with the opaque substance of the disc. I have, not, however, had the means in more recent times of making a sufficiently careful examination of the cicatricula in this condition to enable me to state more minutely in what respects it differs from that of the fecundated egg.

In the ovarian yolk, while still within its capsule, a white spot corresponding to the cicatricula also exists, and occupies the same place in relation to the yolk cavity and canal. Its structure and appearance, however, are somewhat different from that of the true cicatricula of the egg which has passed through the oviduct; it is covered by a layer of closely set nucleated cells which lie below the vitelline membrane; it contains the germinal vesicle in its centre, and, instead of being thinnest towards the middle, the mass of its granular substance is accumulated in greater quantity in that part round and below the germinal vesicle, and thins gradually off towards the margin. Nevertheless, its much lighter colour than the surrounding part of the yolk makes it always easy to distinguish it. Its margin, however, is not so well marked as that of the true cicatricula; for the opaque whitish substance seems there gradually to pass into or be continuous with the most superficial layer of cells covering the yolk. To this ovarian representative of the cicatricula, Von Baer has given the name of *stratum proligerum*. It is also somewhat smaller than that of the laid egg. It is usually to be found on that part of the yolk which is next the ovary, which, as the yolk hangs within its capsule in the usual attitude of the bird, will be uppermost, and for the most part is situated close to the pedicle of the ovarian capsule. This position is not, however, a constant one; for sometimes the cicatricula is seen on the sides of the yolk, or towards the stigmatic band of the capsule, but rarely, it would appear, towards the ends or poles of the yolk.

Fig. 51.



Cicatricula, and its contents, in the ovarian egg of the Fowl.

A. A square portion of the surface of the ripe ovarian yolk, showing the vitelline disc or cicatricula, with the germinal vesicle in the centre, magnified about six diameters.

B. Lateral view of the same, to show the convexity produced by the thickness of the disc round the germinal vesicle.

C. Vertical diagrammatic section of the same; *m*, vitelline membrane; *d*, granular disc; *g*, germinal vesicle.

D, E, F. Germinal vesicles more highly magnified; D, from a yolk of about one tenth of an inch diameter, showing scattered globules or germinal spots; E, from a nearly ripe yolk, quite clear; F, from another of the same period, exhibiting a turbid or minutely granular mass from the action of water.

The cicatricula may generally be perceived on the surface of the yolk when the outermost layers of the capsule have been removed, and the germinal vesicle can be distinguished in it shining through the inner layer of the capsule and the vitelline membrane. It is placed close below the nucleated cells which line the latter, and adheres along with them somewhat to its inner surface; so that in general, it is easiest to remove this disc along with a portion of the vitelline membrane, when it is desired to obtain it for separate and more minute observation by transmitted light. The vitelline membrane being cut round with scissors at a short distance from the margin of the disc, the parts are floated off in water or serum, and then may readily be separated with a little careful manipulation.

The germinal vesicle, or vesicle of Purkinje, may always be seen with the unassisted eye, with a good light, in the centre of the ovarian cicatricula, or proligerous disc, in all ripe ovula, and in most of those which are above a tenth of an inch in diameter. It constitutes there a well-defined shaded circular spot, from $\frac{1}{80}$ to $\frac{1}{60}$ of an inch in diameter. When the proligerous disc alone has been removed for observation and laid on a flat surface, and viewed somewhat from the side, or when the granules are torn asunder with needles, so as to make a partial section of it without removing or bursting the germinal vesicle, it is easy to perceive that the middle part, containing the vesicle, is more elevated than the rest; and that, although the substance of the disc seems to pass quite smoothly or evenly from the sides over the germinal vesicle, the granules of the disc envelope the vesicle only slightly, and none cover its middle part: the vesicle, therefore, is set, as it were, in a depression of the disc, which fits round and overlaps its margins, and a considerable thickness of granular substance is continued in the disc below the vesicle. (See *fig.* 51, in section).

If we select for examination the most advanced yolk of the ovary, which, in a hen laying daily, or almost daily, would probably have been discharged from the capsule in a few hours, we may find some difficulty in isolating the vesicle of Purkinje from the granular disc; for, by this time, the vesicle has become flaccid, weak, and flattened down, and has begun to be softened and dissolved, preparatory to its complete disappearance, which generally occurs about the time when the stigma of the capsule opens to allow of the escape of the yolk into the infundibulum which embraces it. But, in all the other yolks down to those of $\frac{1}{10}$ of an inch in diameter, it is quite easy to break up the granular disc with needle points, and to preserve the vesicle uninjured. We may then free it entirely from adhering granules, and cause it to roll along in the fluid in which it is immersed, or on a plate of glass; and we may perceive that it is a simple membranous vesicle filled with fluid, and without any very obvious granules or nuclei. In the perfectly fresh state, the contents of the vesicle are almost limpid, exhibiting only a slight turbidity scarcely amounting to a granular deposit, provided it has been placed in a medium which does not change its appearance; but, if it is allowed to remain a short time in water, and still more if it is immersed in fluids which coagulate albumen, its interior speedily assumes a minutely granular aspect. The external wall of the vesicle then separates somewhat from the spherical granular mass within; and I have sometimes seen (as represented in *fig.* 51, F) a considerable condensation of the granular mass, so as to leave a large clear space between it and the external vesicle, and give it very much the appearance of the yolk mass in the ova of some small animals within the vitelline membrane. This change seems to be a combined effect of the condensation of the granular mass and the imbibition of fluid by the external vesicle. In the earlier ovula this rounded molecular mass is of proportionately smaller size; and although it differs very much from the smaller nucleus or macula contained in the germinal vesicle of the ova of many other animals, there can be little doubt that it is derived from this structure, as will appear from what is hereafter said of the progress of its development.

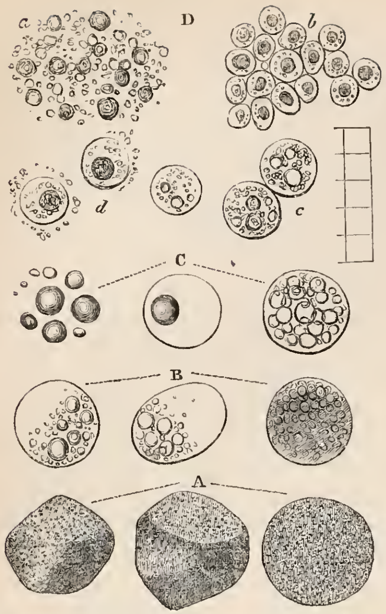
When the yolk has passed into the oviduct, and, in most instances, probably even sooner, or when it has entered the infundibulum, the germinal vesicle has entirely disappeared. Sometimes it is already gone before the opening of the ovarian capsule. The cicatricula then presents an irregularly broken appearance in consequence of the want of support from the wall of the vesicle, and the diffusion of the contents of the vesicle over the surface of the proligerous disc. The solution of the wall of the vesicle is probably a gradual process connected with the state of complete maturation of the ovule. It occurs, as is well known, in the unfecundated as well as in the fecundated egg, and cannot, therefore, in itself, be dependent on the action of the spermatozoa; neither is it altogether caused by the mechanical pressure to which the yolk is subjected in issuing from the ovarian capsule, nor by the pressure of the oviduct itself; for it usually begins, and is sometimes completed before these causes can operate.

The diffusion of the germinal substance from the vesicle (which in the fowl must have already received the spermatic influence in the ovary) has the effect thus of mingling with the remainder of the cicatricula, a material which, it can scarcely be doubted, exerts some immediate influence in inducing the change of segmentation and subsequent process of organisation by which the blastoderm is produced.

Microscopic structure of the ovum. — The investigation of the microscopic structure of the yolk is attended with considerable difficulty, in consequence both of the variety and the delicacy of the organised elements of which it consists. The following parts require our separate attention — viz., 1st. The yellow or external yolk substance; 2nd, the substance of the cavity and canal; 3rd, that of the cicatricula and cumulus; 4th, the vitelline membrane. We shall consider these both in the laid egg and in the ovarian capsule.

1. From the effect of boiling the yolk, every one is familiar with the fact that its yellow substance is coarsely granular; but the exact nature of the small bodies giving this granular structure has not been equally well understood. The examination of this substance with a microscope of moderate magnifying power in a newly laid egg, shows that almost all of the deeply coloured part of the yolk consists of spherical corpuscles of considerable size, so closely set together that they are mutually compressed; and thus, when the yolk has been hardened by boiling, the substance of the corpuscles being coagulated by heat, they present polyhedral forms; but when diffused in fluid in the unboiled state, they are all nearly or quite spherical. The size of these corpuscles varies between $\frac{1}{150}$ and $\frac{1}{500}$ of an inch; but the greater number of them are more near $\frac{1}{200}$ or $\frac{1}{250}$. Some have described the yolk corpuscles as floating in a fluid; and no doubt in the earlier condition of the yolk, a considerable quantity of fluid exists, but in the more advanced condition the amount of mutual compression they exert when coagulated is sufficient to show that its quantity must be very small indeed. Those who have described the yolk substance as mainly consisting of a fluid holding in suspension a quantity of extremely minute granules or molecules, together with some larger corpuscles, have probably been misled, by making an examination of the yolk when not perfectly fresh, and when the larger corpuscles have been in part broken up, and thus resolved into the granular fluid of which they consist. There is no doubt that in birds, and in all the large-yolked animals, the deeply coloured vitelline substance, which, in fact, forms the great mass af these ova, consists almost entirely of the large and usually spherical corpuscles just now noticed. In some animals the form is not

Fig. 52.



Microscopic structure of the elements of the yolk and ovarian ovum of the Fowl.

A. Large granular corpuscles of the yellow part of the vitellus; one of them quite spherical, as they are seen when free; two others angular from mutual compression, from a boiled yolk.

B. Various corpuscles found on the confines of the yellow yolk and the cavity and canal, showing transition forms to the next set.

C. Clear vesicles containing oil globules and detached oil globules of various sizes from the cavity and canal.

D. From the cicatricula; *a*, various-sized granules and globules forming the vitelline disc of the yolk before its discharge from the ovary; *b*, the organised nucleated cells forming the upper layer of the cicatricula in a laid egg; *c*, larger cells of the lower layer; *d*, cells of the cicatricula from an egg in its descent through the oviduct in process of formation. A scale with divisions of $\frac{1}{1000}$ of an inch is appended.

spherical; as, for example, in the cartilaginous fishes, in which a remarkable variety occurs of a cubical form, and sometimes these mixed with tetrahedral forms, as in the skate.*

When free, these corpuscles in the yolk of the bird's egg roll easily on the surface of a plate of glass as perfectly distinct spherical bodies. They present (see *fig.* 52, A) a minutely molecular or granular aspect, but with quite a smooth outline or margin to the whole corpuscle. If subjected to pressure, or cautiously ruptured with needle points, they break readily at one or more places, and allow the escape from their interior of the thick granular fluid, which flows slowly out of them in a stream. The granules are in large quantity, as compared with the fluid in which they are suspended, and are most of them of an extremely minute size, probably below $\frac{1}{30000}$ of an inch in diameter.

* See Müller's Physiology, vol. ii.

Although the yolk corpuscles present the distinct external margin now mentioned, and thus constitute capsules containing the granular fluid, yet we cannot, in most instances, detect any vesicular membranous envelope surrounding them. One may sometimes observe a delicate limiting line; but it has been impossible for me to determine whether it consisted really of a membrane or of a thin condensed layer of the granular substance or plasma containing it. At an earlier period it is probable that these corpuscles have membranous envelopes, but when fully formed the greater number are certainly destitute of them; for occasionally a larger corpuscle may be observed to divide into smaller ones, the outlines of which are nearly as distinct as that of the larger corpuscles.

Nor is any nucleus in general to be perceived in these corpuscles. I have occasionally seen in those from which the granular matter was escaping, and which had thus become less opaque than usual, a slight appearance of a clear hyaline circular space, but it scarcely deserved the name of nucleus; and if these spherical bodies are to be regarded as cells, which I think they ought, it must be in a somewhat different acceptation from that in which the term cell has hitherto been generally applied to vesicular organised structures. But recent researches on the early condition of cells seem to have rendered it necessary that we should include under this denomination several simple spherical minute forms of organised or organising matter, which were not at first regarded as true cells by the authors of the cellular view of organic structure; and when we consider the mode of their formation, it is more than probable that the vitelline corpuscles now under consideration may be included among the number.*

They probably constitute, at all events, as Schwann has first shown, one stage of development of a cellular structure; and, in the meantime, they may with propriety be styled the larger granular yolk corpuscles.

There is considerable uniformity in the appearance and structure of these corpuscles in nearly the whole of the deeper-coloured portion of the yolk; but immediately below the vitelline membrane, several layers of them are of a smaller size, and the outermost layer of all consists of cells which are much smaller and more compressed, distinctly nucleated and of a short cylindrical or prismatic shape. In some places also, corresponding to the concentric lighter lines which run through the yellow yolk, some approach is seen to the next kind of yolk cells or corpuscles, which I shall have to describe—viz., those of the cavity.

The substance of the yolk-cavity and canal, which in the unboiled egg may be distinguished from the other part by its lighter

* The above observation has a general application to such minute spherical masses of matter as are destitute of external envelope or nucleus: but in reference to the corpuscles of the yolk, I ought to observe that Schwann regarded them as cells in various stages of growth.

colour, and in the boiled egg by its softer consistence and less granular appearance, is found by microscopic examination to consist of organised corpuscles floating in a larger portion of fluid, and different from those of the external part of the yolk. The transition from the one kind of corpuscles to the other in these two portions of the yolk, is not sudden; but many gradations of intermediate forms are to be met with on the confines of the two regions.

In the central part of the cavity or latebra, which, when boiled, appears like a thick milky fluid, corpuscles very different from those of the external part are to be found (see *fig.* 52, c). They are almost all of a very regular spherical form with a delicate and clear, but distinct vesicular wall; the interior of the vesicle is occupied by a perfectly limpid fluid, and by one or several highly refracting globules of various sizes, not exactly similar to nuclei, but rather like oil globules, floating within the cell and moving with freedom from one part of it to another. The diameter of the clear vesicles varies from $\frac{1}{700}$ to $\frac{1}{400}$ of an inch, the most being about $\frac{1}{500}$; therefore about half the size of the granular corpuscles of the yellow yolk. The internal oil globules are of very various sizes, the largest being generally about a third or a fourth of the diameter of the enclosing vesicle. Mingled with these vesicles, there are also floating in the fluid of the yolk cavity in considerable numbers, but in less quantity than the vesicles themselves, a set of simple highly refracting globules, exactly similar to those contained within the vesicles from which we may suppose they have been set free. These oil-like globules are of every variety of size, from the minutest point up to $\frac{1}{1200}$ or $\frac{1}{1000}$ of an inch. Towards the surface of the yolk cavity and canal, and extending below the cicatricula, where the vitelline substance gradually passes into the darker yellow yolk, the microscope shows some mixture of and transitions between the several cells or corpuscles before described, those of the intermediate structure being in greatest numbers; these exhibit very various gradations of deposit within them, from the finest granular particles in some, to larger and fewer oil-like globules in others. In most of these transition corpuscles a delicate vesicular wall is perceptible. In the more advanced of these transition forms, as the minute granules are in the process of uniting into larger and larger oil globules, and at last coalesce into a very few or into a single one, the condensation of the exterior layer increases to form a vesicular wall, and a separation of an albuminous fluid from the oil globules takes place within (see *fig.* 52, B). It is these vesicular globules of the cavity which, according to Reichert, are the more immediate source of additions to the germinal membrane in the course of development; for the cavity and canal expand, as it were, at the expense of the yellow yolk, and as these inner globules increase the extension of the haloes and change of colour of the yolk in the first days of incubation spreads rapidly over its surface below the germinal vesicle.

3. *Cicatricula or proligerous disc.* — There does not appear to be any marked difference as to the minute structure of the mass of the yolk and its cavity in the newly laid egg and in the mature ovarian ovulum; but the cicatricula undergoes a great change during the passage of the ovum through the oviduct, which is indicated in a marked manner by the difference in its microscopic structure. During this period, besides the loss of the germinal vesicle, the cicatricula has undergone the peculiar process of segmentation and cell formation, upon the details of which it is my intention to return in connection with the special history of that process in the ovum of mammalia, batrachia, and other animals. The cicatricula of the laid egg is, in fact, after having undergone this process, the organised blastoderm or germinal membrane in which, under the influence of the heat of incubation, the rudiments of the embryo take their origin. It already consists, before incubation, of two layers of organised cells, which are the indication or earliest condition of the upper or serous, and lower or mucous layers, which were described by Pander and Von Baer as taking their origin only after incubation for some hours.* (See *fig.* 52, D.)

The cells of the upper layer are about $\frac{1}{1500}$ of an inch in diameter. They are closely set and very slightly connected together in a continuous layer one cell thick, presenting a smoother upper surface next the vitelline membrane. Each cell consists of an external vesicular wall, a distinct nucleus, and some granular deposit. The nucleus is highly refracting. The cells of the lower layer are nearly double the size of the upper ones, more regularly spherical and less closely connected together. They do not in general present any single nucleus, but rather a small mass of granules and oil-like spherules within them, giving them much of the appearance, though smaller in size, of the corpuscles found between the cavity and rest of the yolk.

In the cicatricula or proligerous disc of the ovarian yolk, on the other hand, containing the germinal vesicle set in its centre, the microscope shows no truly organised cells, but only a mass of simple spherules of very various sizes, but the largest of which for the most part are less than half the diameter of the cells in the upper layer of the blastoderm of the laid egg. They are without any nucleus, and have all the appearance of simple solid spherules from $\frac{1}{3000}$ to $\frac{1}{2000}$ of an inch in diameter, of considerable refracting power, and, indeed, very similar to the nuclei of the cells in the upper blastodermic layer.

Vitelline membrane. — The condensed layer of structureless membrane which has gene-

* The most exact descriptions of the minute structure of the cicatricula are those of Schwann in his Microscopic Researches; of Reichert, in his Beiträge zur heutige Entwickelungsgeschichte, &c.; and Remak, in his Beiträge zur Entwick. des Hühnchens, &c., 1850.

rally received this name in the fowl's egg, and which I have hitherto regarded as corresponding with the immediate membranous investment of the yolk (zona pellucida) in mammalia, and in all animals, constitutes, both in the mature ovarian yolk and in the laid egg, an entire thin transparent covering of the yolk substance, without any aperture that has been discovered in it at any time; delicate and easily torn, but yet of such consistence that under water any portion of it may easily be removed and examined. In the egg which has passed through the oviduct, the vitelline membrane floats free from the cicatricula and surface of the yolk substance; but, so long as it remains in the ovarian capsule, these parts cohere somewhat together; so that, in general, on removing a part of the yolk membrane, a more or less complete lining of the nucleated or outermost layer of yolk cells comes away with it. The microscopic examination of this membrane in the fully formed yolk does not, as already stated, show any very distinct structure beyond an obscure fibrillar and molecular marking, of such fineness, indeed, as to require a high magnifying power (500 to 600 diameters) to bring it into view; and in many parts the membrane appears perfectly homogeneous. In the earlier stages of the yolk's growth, however, we shall see that this membrane is not to be distinguished from the layer of closely set nucleated cells, the outermost part of which appears to become fused together into the membrane as the yolks advance to maturity (see *fig.* 53, K *vm*). We shall presently see that the vesicular envelope which is generally termed the yolk membrane in the bird's egg, and in the ova of all animals possessing the large yolks, is probably a different *structure* from the perfectly homogeneous vesicle which in many other animals arises at a much earlier period of the growth of the ovule, and remains in them as the external covering of the yolk to the end.

Early condition and first formation of the ovarian ovum in birds.—It has already been stated that the ovula exist at a very early period of life in the female bird; constituting in their earliest undeveloped condition minute cells closely surrounded by the simple vesicular capsules and the solid substance of the ovary, which at this period has not lost its primitive compact form. As the bird approaches maturity, a considerable number of the ovula situated nearest the surface increasing in size make an advance in their structure by undergoing certain changes which will immediately be more particularly adverted to. Having attained various sizes from $\frac{1}{20}$ to $\frac{1}{6}$ of an inch, they project slightly as rounded bodies from the surface of the ovary, and remain in this condition till the approach of the breeding season, when some of them destined to reach their full state of development, are at last discharged from their ovarian capsules. A much greater number, however, must remain in the undeveloped condition, awaiting future seasons of evolution; and a very considerable proportion of the whole germs of the ovary rather pass through a retrograde process and gradually disappear without having attained to any considerable size.

Of the smaller or undeveloped ova, such as those of less than $\frac{1}{10}$ of an inch in diameter, some are of a dull whitish or milky colour, the deeper-coloured external yolk substance not having been yet formed, and the yolk substance consisting almost entirely of small spherules or globules, not of true cells or of the granular corpuscles which appear at a later stage. Those between $\frac{1}{10}$ and $\frac{1}{4}$ of an inch are for the most part of a lighter yellow than the larger ovula; but above the latter size the colour has attained nearly its full intensity from the deposit externally of the deep-coloured yolk substance.

In all the ovula above $\frac{1}{10}$ of an inch it is easy to see the germinal vesicle situated on the surface of the yolk, when the capsule is opened, embedded in a more opaque and compact layer of substance which represents the discus proligerus, extending at this period nearly over the whole surface of the yolk. But in those less than $\frac{1}{15}$ or $\frac{1}{20}$ of an inch, the vesicle is not to be seen on the surface. On carefully opening or breaking up the substance of the yolk, the vesicle is easily found in the softer internal substance which flows out from the centre. From the central part of the small ovule, the vesicle appears gradually to pass outwards towards a determinate part of the surface, making its way through the proligerous layer or primitive yolk granules; and thus, in examining ovula at this stage, I have been able to perceive occasionally that the vesicle was situated in a more or less deep depression on the inner surface of that layer, which therefore must be perforated, as it were, by the vesicle in its passage towards the surface. The substance of the disc afterwards collects round the vesicle internally, and is accumulated in greater quantity (cumulus) in that situation. This change of place of the germinal vesicle from the centre or interior to the surface of the yolk in the progress of development of the ovula occurs in some degree throughout the animal kingdom; but it is especially remarkable in the eggs of birds and other animals with large yolks, in consequence of the peculiar connection of the vesicle with the proligerous disc. In the batrachia also, the change is very obvious, and the progress of the vesicle outwards has been well described by Von Baer and others. In this latter class of animals the proligerous layer covers a much greater part, or indeed in most of them nearly the whole of the yolk; but the germinal vesicle occupies always a determinate place in the centre of the layer; showing that the development of the various parts of the ovum proceeds from the first with a fixed relation of position between the germinal vesicle and other parts.

In birds, as in all other animals, the germinal vesicle, which we shall see is the fundamental part of the ovum, is proportionally large in the earlier stage of growth of the ovule, being at the first from a fourth to a half of the diameter of the whole ovule. In the progress of growth, it enlarges somewhat, but only in the earlier periods, and in less proportion than the yolk, and undergoes no farther increase during the greater part of the time that the yolk acquires the greatest addition of new matter. It is worthy of remark, however, that the germinal vesicle is originally of a large size in the eggs of birds and other large-yolked ova; that it is also of very considerable size, even proportionally larger, in the batrachia; and that in mammalia, and other animals with the smaller and granular yolk, its size bears in general a proportion to that of the yolk.

The substance of the yolk appears, in the first place, to be simply granular, or to be composed entirely of minute molecules such as those which always form the yolk in mammalia. These are united together by a somewhat glairy fluid; larger spherules gradually appear among them; and next the distinction between the substance of the proligerous disc and of the yolk cavity becomes apparent. Lastly, the deep-coloured yolk corpuscles are produced, layer after layer being deposited from the exterior, so that the outermost are the last formed. Externally a closer-set layer of nucleated cells covers the surface, in connection with which the vitelline membrane is formed.

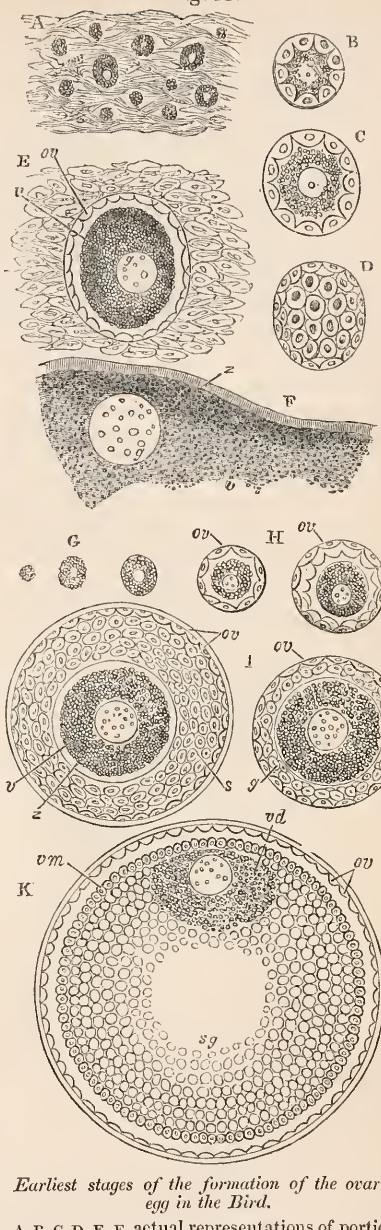
The vitelline membrane is not formed at an early period in the bird's egg: it cannot indeed be perceived in ovula of a tenth of an inch in diameter. We shall presently see that its relations and mode of formation are peculiar in the bird's egg.

Morphology of the bird's egg as ascertained from its first origin and development. — The ovaries of the common fowl, and indeed of most large birds, are less favourable for the investigation of the first origin and earliest condition of the ovule, than those of the smaller tribes; this arises, not so much from the dense structure of the ovary in the undeveloped state, as from the great opacity produced in the ovules themselves, almost from the first, by the deposit of thick-set yolk granules. In some of the smaller singing birds, the thrush, yellow-hammer, or chaffinch, the parts are clearer and more transparent; and it will be found that the phenomena of earliest formation are most easily investigated in them.

According to Dr. Martin Barry's observations, in birds as well as in other animals, the germinal vesicle is the part of the ovum which is first formed. In the pigeon and common fowl, he has observed these vesicles in the ovarian substance at a very early period*; and he believes their origin as simple cells to precede that of the ovarian vesicles, or follicles, or, as he has termed them, ovisacs, which surround them at a somewhat later period, but still in the earliest stages of the formative process. By other observers the ovarian vesicles have

* See Philos. Trans. for 1838, p. 309. In this, coinciding with the opinion previously expressed by Von Baer.

Fig. 53.



Earliest stages of the formation of the ovarian egg in the Bird.

A, B, C, D, E, F, actual representations of portions of the ovarian stroma and ovisacs of the thrush; G, H, I, K, diagrammatic sections of the same. A. In the ovarian stroma are seen the earliest state of the ova and ovisacs that can be perceived, consisting, first, of minute granular spots; next, of clear points within a minute granular mass; and third, of small germinal vesicles, surrounded with the minutely granular dark yolk substance. Compare with G, in the diagrammatic figure.

B and C. Different stages of formation of the ovisac round the small ova: the epithelium is seen to line the sac: the germinal vesicle with occasionally a single macula is now apparent. D. The epithelium of the ovisac shown in focus over the whole surface: in the other figures it is only shown in focus at the margin. E. The ovisac and ovum more advanced; *o, v*, ovisac, with epithelial lining; *v*, minutely granular yolk; *g*, germinal vesicle.

F. Part of an ovule of $\frac{1}{40}$ of an inch in diameter highly magnified: *v*, minutely granular or primitive yolk substance; *g*, germinal vesicle; *z*, thick consolidated membranous layer which formed a vesicular covering for the primitive ovule, and which corresponds to the zona pellucida of the mammiferous ovule.

I and K are intended to illustrate, diagrammatically, the view, that after the disappearance of the zona, and the formation of larger granular yolk cells, the outer layer of the cells of this substance forms the permanent vitelline membrane of the bird's egg; *v, d*, remains of minutely granular yolk, forming the vitelline disc round the germinal vesicle; *s, g*, large corpuscles of the yolk; *v, m*, outer layer of the cells of the same, on which the vitelline membrane is afterwards formed.

been looked upon as the primitive or first-formed structures connected with the origin of the ova, the germinal vesicles subsequently making their appearance within them. We shall return to this point hereafter in connection with the history of the mammiferous ovum. My own observations agree with those of Barry, as I have sometimes observed very small germ-vesicles or cells in the ovarian stroma without any follicular covering. But it must be admitted, at the same time, that in birds the ovisac or ovarian vesicle is formed so early that it is observed almost always coexisting with the germinal vesicle or rudiments of the ovule; so that, if the latter takes the precedence of the ovisac, it must be by a very short period.

According to Barry, there is seen almost from the first, in the clear germinal vesicle, a minute distinct granule or round spot, which constitutes the first state of the macula germinativa. Very soon the vesicle is surrounded by a small quantity of a clear fluid in which are rapidly deposited globules or granules constituting the first rudiments of yolk substance. There is no vitelline membrane, however, in birds, at the first; nor are the larger cells which at a later period intervene between the ovisac and the primitive yolk, formed in the earliest stage. The smallest ovisacs which Barry observed, and which consisted of perfectly simple vesicular linings of the cavities containing the rudimentary ova, in the pigeon and common fowl, were from $\frac{1}{600}$ to $\frac{1}{300}$ of an inch in diameter.* At a somewhat later period, the number of maculæ (nuclei) in the vesicle, and of the yolk granules externally, had increased, and a delicate membrane, which he describes as vitelline membrane, and believed apparently to be the same which afterwards surrounds the large yolk in the fully-developed ovum, has made its appearance. At this period also there begin to be formed within the ovisac a set of larger nucleated corpuscles or cells, which are external to the true ovum, and which may be considered as corresponding with the so-called granular contents (substantia and tunica granulosa) of the Graafian follicle in mammalia.

The early structure and development of the ovum of birds have more recently been described, with considerable detail, from observations on the chaffinch and common fowl by Dr. H. Meckel*; and as the observations of this author have led him to take a somewhat different view of the relations of some of the parts of the ova of birds and other animals from that which has hitherto been generally adopted, it will be proper to give a particular account of them in this place. Many physiologists have felt the incongruity of the comparison generally made between the minute and simple ovum of the mammifer, and the large and more complex yolk of the bird, and most are disposed to acknowledge the necessity of making some more marked distinction between the granular and the cellular yolk substance in the two great groups to which these ova respectively belong. It has before been stated, that Von Baer on his discovery of the mammiferous ovum, regarded it as corresponding, not to the whole ovum of birds, but to the vesicle of Purkinje. The discovery, in 1834, of the germinal vesicle in the mammiferous ovum, of the existence of which Von Baer had no distinct knowledge, induced Valentin and others to maintain that the essential parts of the ovum are the same in the bird and the mammifer. But it may be doubted whether physiologists may not have proceeded further than they were warranted by observation in regarding the vitelline membrane and large corpuscles of the yellow yolk of birds as essentially corresponding parts with the zona pellucida and the smaller granular yolk of the mammifer. For the membrana vitelli of the bird's egg may, perhaps, be more analogous to the outermost layer of the membrana granulosa of the Graafian follicle, and the large cellular yolk to a part of the same substance or the fluid of the Graafian follicle; while the minutely granular yolk in which the cicatricula originates and the germinal vesicle together are the true representatives of the small ovum of the mammifer. It seems undoubted, that what we term the yolk membrane in the fowl's egg does not exist in the early stages, and is formed indeed only as the ovarian egg approaches maturity, and it is admitted that no large cells similar to those of the bird's yolk exist within the cavity of the zona pellucida of the mammiferous ovum. If this view is correct, we may expect to find a representative in the egg of the bird and of other animals having similar ova, of the very marked enclosing vesicle, which has received the name of zona pellucida

* Vide loc. cit. Plate v., figs. 18, 19, and 22 of pigeon; figs. 23 and 24 of common fowl. The membrane which Barry described as vitelline in the earliest stages of growth of the bird's egg was probably not so, but the outline merely of the albuminous substance in which the primitive yolk granules are deposited. This will be made more apparent in our description of the formation of the ova of Batrachia.

* See his paper, Die Bildung der fur partielle Fürchung bestimmten Eier der Vögel, &c., in Siebold and Kölliker's Zeitsch. für Wissenschaft. Zool. vol. iii. p. 420, 1852.

in the mammiferous ovum. Now, according to H. Meckel there is, not from the very first, but in the earlier stages of formation of the yolk of the fowl and of other birds, a homogeneous vesicular membrane enclosing the primitive or granular yolk, or what he terms the true egg substance. As the cellular yolk is formed, this membrane, to which he thinks himself warranted in giving the name of zona pellucida, disappears, and already in ova above $\frac{1}{10}$ of an inch there is no trace of it left.

The observations of H. Meckel on this subject appear to be both novel and important; but he has not been equally successful in the theoretical deductions made from them. In the commencement of the paper before referred to, he thus announces his view of the morphology of the bird's egg: "For a right and consistent nomenclature and definition, we must designate the corresponding parts according to their analogy with those of the human body. I believe, therefore, that that alone ought to be regarded as the true egg which exists in Man, Mammalia, Naked Amphibia, and Osseous Fishes; and that in the remaining Vertebrata the ovum consists only of the so-called vesicle of Purkinje, and that all the other parts are accessory, superimposed, and unessential. In particular, that the yellow yolk of the bird and scaly reptile is analogous to the corpus luteum of the human ovary, the albumen ovi to the uterine secretion, and the calcareous shell to the decidual mucous membrane of the uterus." Von Baer, at p. 32. of his Epistola, uses the following words, which have been much controverted by some of those coming after him, but which show that he was aware of the difference in the relation of parts in the birds and mammiferous ovum: "Vesicula ergo Graafiana cum ad ovarium generatimque ad corpus maternum respiciamus, ovum sane est Mammalium, sed evolutionem quod attinet, vehementer discrepat a reliquorum ovo animalium," &c. And again, "In mammalibus vesicula innata vitellum magis excultum continet, et ratione ad fetum geniturum habita verum sese probat ovum. Ovum fetale dici potest in ovo materno. Mammalia ergo habent ovum in ovo; aut, si hac dicendi formula uti licet, ovum in secunda potentia." Both in the Epistola, and the Commentary upon it, Von Baer insists strongly on the analogy between the cellular substance of the Graafian follicle and the yellow yolk; and he seems to have erred chiefly in limiting his comparison of the mammiferous ovum (within the zona) to the vesicle of Purkinje of the bird's egg. If, therefore, we modify Von Baer's view so much as to regard the vesicle of Purkinje along with the granular cicatricula of the bird's egg, as corresponding to the whole of the mammiferous ovum, and the granular cells (tunica granulosa, &c.) of the Graafian vesicle as corresponding to the yellow yolk (the zona pellucida having disappeared in the bird's egg), we shall establish a more correct relation of the parts than that suggested by H. Meckel. I am not aware of any animal in which the germinal vesicle alone, without some yolk substance and an external inclosing membrane (zona, or vitelline membrane) forms the entire ovum.

I will now state the result of my own observations on this subject, by which I conceive is proved the correctness of H. Meckel's view, that in birds there is a primitive ovum, enclosed within a zona, distinct from the large mass of cellular yolk, which is formed at a later period.

As soon as the membranous wall of the ovisac or ovarian follicle has become distinct in the ovary of the fowl, we can perceive at the same time a layer of larger cells lining it which form a clearer ring round the opaque ovule. The ovule itself consists then merely of the germinal vesicle and a small quantity of the primitive yolk substance. The latter becomes opaque at so early a period that it in general hides completely the germinal vesicle. It seems to arise by the deposit of very fine granules, probably of an oily nature, in a dense albuminous fluid or blastema which collects round the germinal vesicle very soon after the latter is invested by the ovarian follicle. In follicles of $\frac{1}{100}$ of an inch in diameter the primitive ovule, the membrane of the enclosing follicle, and between them the layer of larger clearer cells, are all perceived with facility. There is not yet, however, any investment of the ovule comparable either to a zona pellucida or vitelline membrane.

In ovarian follicles of $\frac{1}{30}$ or $\frac{1}{40}$ of an inch in diameter, a farther progress is to be perceived. On bursting any such follicle with fine needle points, the ovum is ruptured, and the germinal vesicle usually first escapes along with the more fluid internal part of the yolk, in which it is freely suspended. This vesicle is about $\frac{1}{130}$ of an inch in diameter, presenting externally a smooth, thin and delicate vesicular membrane of a spherical form, of which the double outline is just discernible with a magnifying power of 300 diameters. The vesicle is partly filled with fluid and partly with a finely granular spherical mass of no great opacity, which corresponds to the macula germinativa. In most instances this mass occupies about two thirds of the diameter of the vesicle. The yolk substance, which has scarcely altered from its primitive opaque finely granular condition, now consists of a more fluid internal part containing fewer granules, and in which the germinal vesicle floats, and of a more consistent external part. In the latter a manifest change has occurred in this respect, that towards the outer surface there is separated a much clearer ring of substance contrasting strongly with the more opaque part. This may with correctness, it is true, be described as a membrane, as H. Meckel has done in comparing it with and giving it the designation of the zona pellucida. But the very remarkable structure, which the author now mentioned has had the merit of first pointing out, is one deserving of the greatest attention. It has appeared to me to be gradually formed in ovula of about $\frac{1}{80}$ or $\frac{1}{60}$ of an inch in diameter, by the clearing and partial consolidation of the outermost part of the albuminous basis or blastema in which the granules of the primitive yolk substance are deposited. It is at first comparatively thin: it is most apparent by its greater clearness and consistence in ovules of $\frac{1}{40}$ or $\frac{1}{30}$ of an inch in diameter, in none of which have I ever failed to observe it. In those of $\frac{1}{20}$ it becomes broader, but less clear and somewhat softer in its consistence, and is uneven and as if softening away or breaking up on the external edge; and in ovules of $\frac{1}{10}$ of an inch it has in general disappeared. At no period have I observed it to assume the glassy transparency, nor has it the distinct outline and membranous appearance represented by H. Meckel; but it seemed rather like a portion of the albuminous basis of the yolk substance, nearly but not quite deprived of the granules, which are thickly deposited in the rest.

While these differences are stated, however, it appears to me warrantable to coincide in so far with the view of H. Meckel as to regard this structure as a temporary representation in the fowl's egg of the zona pellucida, which in the mammiferous ovum assumes greater consistence, passes into the membranous form, and constitutes the only ovarium covering of the ovule.

In ovules of $\frac{1}{30}$ to $\frac{1}{20}$ of an inch in diameter, the layer of nucleated cells placed between the primitive ovule and the membrane of the follicle, and which may be looked upon either as a cellular lining of the follicle or a peculiar investment of the ovule, has become more distinct and consistent, and the cells of the outermost layer have assumed the form of short compressed prisms. They have finely granular contents and clear nuclei, with one or sometimes two nucleoli, like the cells of the tunica granulosa of the mammalian follicle. It appears that these cells come afterwards to form the external part of the yolk of the bird's ovum, the cellular part of the yolk being formed within them, and the vitelline membrane being produced on their outer surface.

The bird's ovule, it is well known, usually fills completely the ovarian follicle; but in several instances I have observed, from imbibition of water or some other cause, the ovule to occupy not more than half the diameter of the follicle, the remainder being filled with a clear fluid; and in these instances the prismatic layer of cells adhered closely to the surface of the zona and primitive granular yolk.

In ovules of from $\frac{1}{20}$ to $\frac{1}{10}$ of an inch the formation of the vitelline membrane appears to commence. The external nucleated cell covering has increased in quantity, and adheres more closely to the granular yolk, with which it generally comes away when the follicle is opened. The external edge of the layer of prismatic cells, the length of which is considerably increased, is now surrounded by a narrow pellucid space enclosed by a double line, presenting the appearance as if a small part of the bases of these cells had been fused together in a homogenous film. This is the commencement of the formation of the true vitelline membrane, which in the latest period of ovarian growth of the ovum becomes nearly quite structureless, but which throughout the greater part of the process retains somewhat of the hexagonal marking from the close adhesion of the cells by the amalgamation of a part of which the membrane has been produced.

In follicles of about $\frac{1}{10}$ of an inch or larger the true cellular elements of the yolk have begun to be formed. The manner in which these originate I have not as yet had the means of determining with precision. They appear, as H. Meckel has suggested, to be produced as a secretion from the interior of the ovarian follicle; but they are more immediately formed within the layer of prismatic cells which envelope the whole ovule. Nor have I been able to determine their precise relation to the zona and primitive fine granular yolk. When the zona has disappeared, as is usually the case in ovules of $\frac{1}{10}$ of an inch, the cellular elements of the yolk seem to begin to mingle with the finely granular substance. At first, cells and larger oil globules, similar to those of the yolk cavity, are produced. So long as these alone exist, the yolks have a dull milky-white aspect. Later, or in those of $\frac{1}{6}$ of an inch, or even somewhat smaller, the yellow tinge appears, and this very soon becomes more decided, at the same time that the peculiar large granular corpuscles or cells are formed in which the vitelline colouring matter principally resides. These corpuscles are produced in successive layers within the layer of prismatic cells of the external tunic; and it is probable that there is some periodical variation in the rapidity of their formation from the alternation of concentric layers of deep yellow corpuscles with those of a lighter colour which may be observed in the section of a boiled yolk. The corpuscles of the yellow yolk are not, however, formed in equal quantity in every part: indeed they are quite deficient at that side on which the remains of the primitive granular yolk with the imbedded germinal vesicle are situated.

With regard to the germinal vesicle, it is to be observed that it is at first quite free in the more fluid internal part of the primitive yolk; in the next stage, before the formation of the cellular yolk, the germinal vesicle comes to be imbedded in the more consistent external part of the primitive granular yolk; and it is, no doubt, chiefly the remains of this which form the germinal or vitelline disc: but further observations are still required to determine the precise manner in which this arrangement of the primitive yolk in the discoid shape takes place.

It appears, further, that in the formation of the elements of the more advanced yolk, the earliest produced, or innermost, remain the softest; the latest formed, or outermost, acquire the greatest consistence. The external layer of prismatic cells next the vitelline membrane passes with it completely round the whole yolk and over the vitelline disc; the next layer, less prismatic and more rounded in their form, but still distinctly nucleated cells, covers the whole surface of the yolk, with the exception of the part occupied by the vitelline disc, with the margin of which this layer is continuous. The next layers passing inwards consist of granular corpuscles, which do not in general present the appearance of nucleated cells.*

In conclusion, therefore, the ovarian ovum of the bird being formed in an ovarian capsule, is at first very similar to the Graafian vesicle of the mammalia, and differs chiefly in the earliest stages from the mammiferous ovum in the proportionally large size of the germinal vesicle, and in the absence from this vesicle of the more distinct and persistent nucleus which exists in animals having the smaller yolk. This germinal vesicle may be looked upon as the fundamental part of the ovum in both kinds of animals. Along with it there exists, from a very early period in birds, a granular opaque yolk substance. This substance by itself constitutes the whole yolk of mammalia; but in birds it probably remains as a part, if not the whole, of the proligerous disc (afterwards cicatricula). The mammiferous ovum is closely surrounded at an early period with a dense transparent membrane (the zona pellucida) formed by a condensation of the outermost layer of the albuminous part of the yolk; and a similar envelope, but less dense, exists in the earlier stages of formation of the fowl's egg, surrounding the finely granular primitive yolk substance along with the germinal vesicle. In both birds and mammalia the ovarian follicle, besides being lined with a layer of epithelial cells, secretes, or has formed immediately within it, a quantity of nucleated granular cells more loosely united together, known in mammalia by the somewhat inappropriate names of tunica granulosa and substantia granulosa of the ovarian follicle. But in birds, although this substance is at first somewhat similar in structure and relations, cells afterwards increase within it in very large quantity, and acquire a peculiar structure and colour, constituting the yellow part of the yolk substance. The outer covering of the yolk, or vitelline membrane, is only produced when the ovule has attained considerable advancement, by a new deposit upon the external surface, or by the condensation of a part of the external layer of these cells, which covers the whole yolk, together with the cicatricula. The germinal vesicle is fixed in the bird's yolk, towards the surface, in the proligerous disc. In the mammiferous ovum the germinal vesicle is, for the most part, near the surface of the yolk substance, but not so far as is known in a determinate situation, and the whole ovum in its zona pellucida is fixed in the tunica granulosa towards that part of the follicle which is next the surface of the ovary.

The germinal vesicle bursts or is dissolved in both. In mammalia it is probably diffused through or over the whole granular yolk: in birds it probably overspreads only the proligerous disc. The whole yolk is segmented in mammalia, while in birds this process is confined to the proligerous disc, out of which the blastoderma is produced.

The full description now given of the structure of the bird's egg will enable me to treat comparatively briefly of that of other animals. In regard to most of them, indeed, it will scarcely be necessary to do more than to notice their most important peculiarities.

Before leaving the ova of the first group, it may be noticed on the authority of Leuckart*, that in the scaly reptiles there is not the same difference between an external coloured yolk and the lighter cavity as in birds, but that the whole yolk substance is of a paler colour, and of a more clear and uniform appearance. Still from a preponderance of oily matter in the vicinity of the cicatricula, there is the same tendency to that part of the ovum floating uppermost. The germinal vesicle in the ovarian ovum of these animals presents at an early period a very subdivided condition of the macula; and it is placed in a granular disc, which does not appear to differ essentially from that of birds. The vitelline membrane is equally structureless. Leuckart has traced the development of the ovum in Lacerta crocea and Coluber lævis, and has ascertained that in them, as in birds, the primitive yolk substance is destitute of cellular elements, and has at first no special covering. The true or external vitelline membrane is probably formed, precisely as in birds, on the exterior of the outermost layer of the cellular part of the yolk.

In the cartilaginous fishes there is a greater departure from the type of structure now described. The external vitelline membrane is of

* While the above was passing through the press, I received the 27th and 28th parts of R. Wagner's Handwörterbuch der Physiologie, containing the Article "Zeugung," by Professor Leuckart of Giessen. I regret that I have not previously had the advantage of perusing the very luminous and comprehensive sketch, by that author, of the structure and morphology of the ovum of different animals. As, however, Professor Leuckart has stated that his observations do not confirm the statements of H. Meckel in regard to the zona pellucida of the bird's ovule, I have thought it right, notwithstanding the unfavourable period of the year (October), to repeat carefully my examination of this matter; and I have here to state that, in the common fowl and thrush, the description given above has received the fullest confirmation. While, therefore, I am inclined to differ, as above stated, from the views of H. Meckel as to the morphological analogy of parts of the ovum in different animals, I must admit the existence, at a certain stage, of the very peculiar structure pointed out by him, as corresponding with the zona pellucida, with the differences as to details which I have there mentioned. The primitive ovule of the bird therefore consists of the germinal vesicle, granular yolk, and this so-called zona; and the cellular substance of the bird's yolk, is the product of secretion, or is a modification of epithelial formation from the interior of the ovarian follicle.

* Art. *Zeugung.*

great delicacy, and is perceived only with difficulty. The yolk substance is in great part composed of peculiar angular corpuscles, sometimes flat and tabular, at other times cubical, octahedral, and of other forms. It has been stated by Leydig * that in the plagiostomatous fishes there is no vitelline disc or cicatricula ; but this does not agree with my observations in the common skate fish, in the ova of which I have always observed a very distinct flat disc about three-eighths of an inch in diameter, of a lighter colour than the surrounding part of the yolk, and situated on the surface which naturally floats uppermost. The germinal vesicle, which is larger than that of birds, sometimes $\frac{1}{40}$ of an inch in diameter, is extremely delicate and very easily ruptured. Its nucleus or macula is originally single, but becomes afterwards subdivided or multiple and diffused.

The ova of the cephalopoda, which may, according to most embryologists, be included in this group, are of considerable size. They possess a germinal disc, and the segmentation of the yolk is partial or is confined to that disc, as in the animals previously mentioned.† The large yolk corpuscles are spherical masses of united oil granules, and like the most of those of the bird's egg without any true enclosing vesicle. The germinal vesicle is of considerable size, and has subdivided maculæ. The whole are enveloped by a fine structureless vitelline membrane. In the course of the formation of the ovum, the external part of it undergoes a remarkable change in being folded inwards in numerous deep grooves, which almost reach the centre of the yolk. This folded structure is in the smaller species again effaced before the ova reach maturity, but in the larger species it appears to remain, and to be the cause of a peculiar reticulated marking over the surface of the ova.

In regard to other classes of the invertebrate animals of which the ova may appear to belong to this group, I shall have occasion hereafter to state some additional facts, in explanation of the manner in which in some of them the granular and cellular elements of the yolk are occasionally combined.

From the foregoing considerations, then, it appears that in ova of the first group as distinguished in this treatise, the germinal vesicle is at once the first formed and the fundamental part of the ovum around which the rest of the parts are deposited. It alone, therefore, is strictly to be regarded as a simple or primary cell. It may aptly be called the *Germ-cell.* In birds its nucleus or macula is originally simple, but at a very early period it undergoes subdivision into nucleoli or maculæ, so numerous and minute as at last scarcely to be recognisable, and thus the germinal vesicle loses in such animals somewhat the characteristic cellular structure which it presents in many others. Next, by aggregation of the primitive yolk substance round the germ-cell, and by the gradual consolidation of a clear film on the outermost part of the albuminous matrix of this substance into the form of an enclosing vesicle, there is produced the *primitive ovum*, a secondary cell, in which the zona pellucida constitutes the cell wall, the oil granules and albuminous fluid of the yolk substance the contents, and of which the germinal vesicle is now the nucleus. And lastly, if it is considered desirable to extend the application of the term cell also to the mature state of the ovarian egg of the bird, we may perhaps still regard that organism as a tertiary cell (in the ascending series) formed by the superposition of new parts, some of which are themselves cellular in their origin, round the primitive ovum, the whole being at last enclosed and moulded in the vesicular form by the external vitelline membrane ; a peculiarity of this formation being that in the meantime the wall of the secondary cell or primitive ovum has disappeared. But, notwithstanding the spherical form, the isolated position, and the simple structure of the parts which compose the completed ovarian ovum of birds, doubts may fairly be entertained as to the propriety of bringing such complex organisms under the designation of cell as now generally employed.

§ 5. More detailed description of ova belonging to the second group, or with small granular yolk and complete segmentation.

If the foregoing views are correct, it appears that, while the ova of birds and other animals of the first group contain within the vitelline membrane the whole product of formation which belongs to the ovarian capsule, the ova of mammalia and animals of the second group comprehend only those parts of the contents of the Graafian follicle which are formed within it at the earliest period — viz., the germinal vesicle and the primitive yolk substance with its limiting zona. In the Graafian follicle of mammalia, there is likewise produced a large proportional quantity of cellular elements and albuminous fluid, the tunica and substantia granulosa, &c., in a part of which (cumulus proligerus), the ovum comes to be imbedded in the progress of their formation ; and these superadded contents of the Graafian follicle escape along with the ovum when it leaves the ovary, but do not apparently maintain any long or constant connection with it.

In the ova of those invertebrate animals which belong to this group, the conditions of formation do not admit of their comparison with those of mammalia ; but they agree with them in so far that the first germ-cell is enclosed by a finely granular yolk, and that the vesicular envelope of the ovum generally corresponds to the zona formed by consolidation on the surface of the primitive yolk.

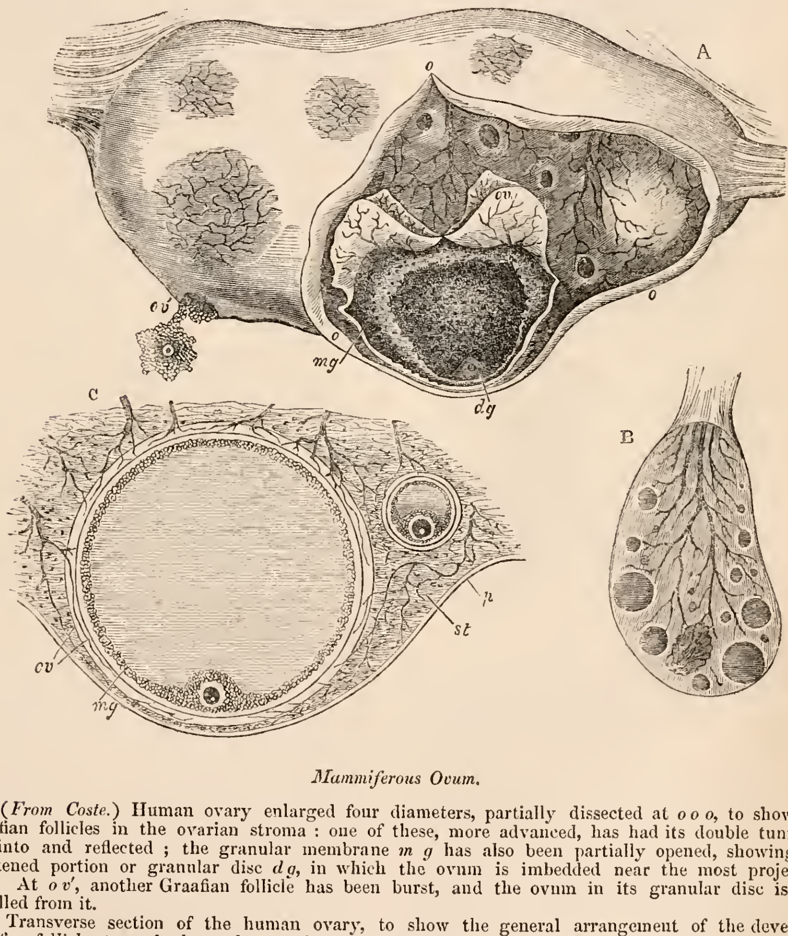
* Beitrage zur Mikroskop. Anat. der Rochen und Haïen, p. 87., a work which I quote only from Leuckart.

† We owe this interesting discovery to Kölliker. See his work on the Development of the Cephalopoda. Zürich, 1844.

Ovum of Mammalia and of the Human Species.— There is a remarkable uniformity in the size, structure, and relations of the ovarian ovum in the whole class of Mammalia, with the exception of the families of Marsupiata and Monotremata; in the last of which especially there is an approach to the oviparous type. We shall first consider the more common form of the mammiferous ovum. Of this the most marked characteristics are, as has already been stated, the very small size in proportion to the ovarian follicle, the finely granular yolk-substance, and the dense, clear, and firm external covering or zona pellucida.

The Graafian follicles, or ovarian vesicles, in which the ova are situated, attain, when mature, a size of from $\frac{1}{50}$ to $\frac{1}{4}$ or even $\frac{1}{2}$ an inch, varying in size in some measure with, but not in exact proportion to, the stature of the animals. In the human ovary these follicles are firm spheroidal sacs, which attain when mature an average size of about $\frac{1}{8}$ of an inch. In the ovaries of women, during the child-bearing period, a number of smaller follicles lie throughout the greater part of the substance of the ovary; the more developed follicles being usually placed towards the free surface, but at some little distance from it. As they enlarge and approach maturity, the ovarian substance appears to give way to them, or to become gradually thinner between the follicles and the outer surface of the ovary, so as at last to leave almost nothing but the covering membranes of the ovary at the most projecting part. Even when of their full size, however, the Graafian follicles of the human subject and of most animals do not project much beyond the general surface of the ovary;

Fig. 54.*



Mammiferous Ovum.

A. (*From Coste.*) Human ovary enlarged four diameters, partially dissected at *o o o*, to show the Graafian follicles in the ovarian stroma: one of these, more advanced, has had its double tunic *o v* cut into and reflected; the granular membrane *m g* has also been partially opened, showing the thickened portion or granular disc *d g*, in which the ovum is imbedded near the most projecting part. At *o v'*, another Graafian follicle has been burst, and the ovum in its granular disc is seen expelled from it.

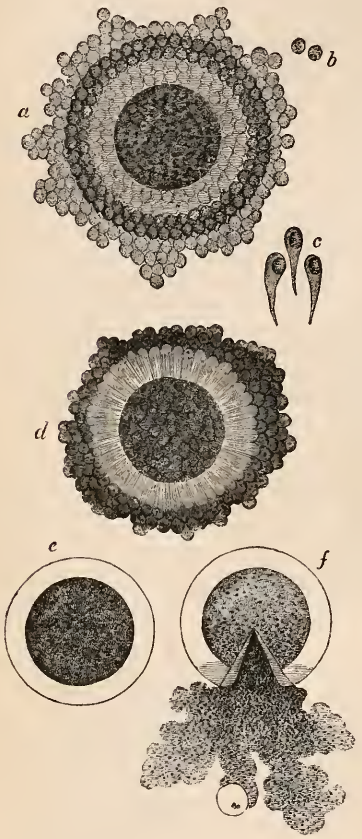
B. Transverse section of the human ovary, to show the general arrangement of the developed Graafian follicles towards the surface; twice the natural size.

C. Diagrammatic representation on an enlarged scale, in section, of two Graafian follicles, in different stages of advancement in the ovary of a mammifer. *p*, peritoneal covering of the ovary; *st*, ovarian stroma; *o v*, the two layers of the ovisac; *m g*, membrana granulosa, near which is the discus granulosus, with the ovum imbedded.

but in some animals, in which the vesicles are proportionately more expanded, they extend beyond the general line of the surface in various places, and even sometimes give the ovary somewhat of the mammillated or grape-like appearance more common among oviparous animals.

The follicle is filled to distension with a clear albuminous fluid, which escapes with force when an incision is made through the

Fig. 55*.



Ovarian ovum of the Dog. (*From Bischoff.*)

a, magnified representation of the ovarian ovum of the dog, nearly mature, situated in the discus proligerus and part of the cells of the granular membrane; *b*, several detached granular cells.

d, another ovarian ovum of the same animal perfectly ripe, immediately previous to the rupture of the Graafian follicle; the cells of the proligerous disc have become of a pediculated shape; *c*, some of these cells detached.

e, the ovum from the same specimen as in *fig. a*, freed artificially from the granular cells of the disc, showing externally the thick clear zona or external membrane, and internally the opaque yolk substance: in the latter the germinal vesicle is obscured by the opacity of the substance surrounding it.

f, the same ovum burst by pressure, showing the contents of the ovum which have escaped, viz. the finely granular yolk substance and the germinal vesicle with its macula.

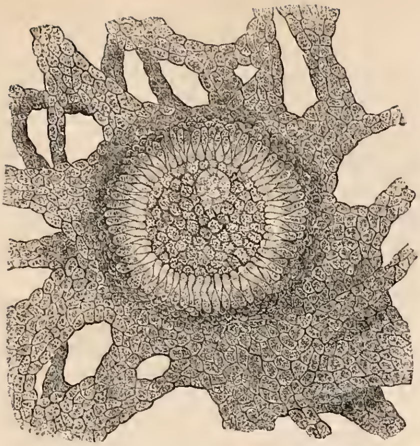
membrane. Close to the inner surface of the follicle, and surrounding the fluid, is situated the layer of nucleated granular cells which has been termed *tunica* or *membrana granulosa*, from the opaque granular appearance of the cells composing it. These cells form a complete vesicular lining of the follicle; but throughout the greater part they cohere with only a moderate degree of firmness, so that the membrane readily tears when the follicle is opened. The minute ovum is imbedded in a thicker portion of this layer, the *cumulus* or *discus proligerus* of Von Baer, and is almost invariably situated close to the inner surface of the most projecting part of the Graafian follicle (see *fig*. 54*. A. and C., *mg*.) where in some animals, but not in the human ovary, the ovum may be detected in the undissected follicle through its coats and the ovarian coverings.

The cells of the membrana granulosa are in general about $\frac{1}{2400}''$ in diameter. They adhere with considerable firmness to the surface of the zona; so that when the follicle is opened and its contents are allowed to run upon a plate of glass for examination, the ovum is always found placed in its disc in a circumscribed attached portion of the membrana granulosa of about twice its own diameter. The ovum is itself of a nearly perfect spherical form when freed from pressure; but as it lies thus imbedded in the membrana granulosa, and moistened on a plate of glass, it gives rise to a slight rounded elevation in that membrane, which may easily be detected with the naked eye when the specimen is viewed sideways.

When the contents of the Graafian follicle are discharged naturally during life, a small aperture occurs nearly in the centre of the most projecting part of the wall of the follicle; and as the ovum lies near this place in the membrana granulosa, it is liable to be evacuated first, along with a portion of that membrane, which is soon torn away from the rest by the pressure of the fluid behind it, impelled by the contraction of the walls of the follicle and surrounding ovarian substance. During the descent of the ovum through the Fallopian tube the cells of the proligerous disc immediately surrounding the ovum alter their form, and are subsequently detached from the zona, so as to leave its external surface quite free and smooth. I have not, any more than Bischoff, been able to observe the four retaining straps or retinacula described by Martin Barry in his first series of Researches, as portions of the membrana granulosa naturally thicker than the rest, and which, radiating nearly at right angles from the proligerous disc, serve, as it were, to guide the ovum and its disc towards the aperture by which it escapes on the bursting of the follicle. The accompanying figure from Coste (56*.) gives that author's view of a structure somewhat similar to the retinacula of Barry.

The size of the mammiferous ovum itself is much more uniform among the different families of Mammalia than that of the Graafian follicle,

Fig. 56*.



Ovum of the Rabbit in the tunica granulosa. (*From Coste.*)

The middle part of one of M. Coste's figures has been here copied to show the peculiar arrangement of the granular cells round the disc and ovum, which according to him are of the same nature with those described by Dr. Martin Barry as *retinacula*. It may be doubtful whether this structure is constant.

and bears no regular proportion in different families of animals to the stature of the whole body. In the mature state this variation extends from $\frac{1}{140}$ to $\frac{1}{260}$ or $\frac{1}{300}''$. The following are the results of a few measurements made by myself and others of the external diameter of the mature ovarian ovum, viz., man $\frac{1}{180}$, dog $\frac{1}{160}$, cat $\frac{1}{180}$, rabbit $\frac{1}{150}$, rat $\frac{1}{200}$, mouse $\frac{1}{220}$, pig $\frac{1}{200}$, cow $\frac{1}{250}$, guinea-pig $\frac{1}{240}''$.

The external tunic, or zona pellucida (a term founded on the description of Von Baer*, from its presenting the appearance of a transparent ring between the opaque granular yolk-mass within and the granular cells externally), is of great proportional thickness; viz., from $\frac{1}{1500}$ to $\frac{1}{2500}''$, or from $\frac{1}{8}$ to $\frac{1}{12}$ of the whole diameter of the ovum. When entirely freed from the granular cells, its external surface appears smooth; and the inner surface, which is exactly parallel to the outer, is also remarkably smooth. The substance of this tunic is very tough, and possesses considerable elasticity; so that the ovum and its zona may be flattened by external pressure to a great extent; and yet it regains its nearly spherical form when the pressure is removed. It is of glassy transparency and homogeneous; neither any laminated, nor fibrous, nor other structure being perceptible under the highest magnifying power. It is easy to obtain evidence that it is one thick membrane, and not composed of two layers with intervening fluid, as some have held, by cleaving it with fine needle-points, when the cut edge becomes fully apparent. It has recently been stated by Remak*, that in the mature ovarian ovum of the rabbit, when freed from the granular cells, radiated lines may be perceived running quite through the zona pellucida; these linear radiations, he conceives, indicate a peculiar structure of the zona, somewhat similar to the perforated condition of the outer membrane of the ovum in osseous fishes. I have perceived some of this radiated appearance; but I am inclined to believe that it depends not on any structure of the zona itself, but rather on the marking produced by the adhesion of parts of the cells of the tunica granulosa, which become pediculated in very ripe ova, and have then a radiated appearance on the zona under pressure; as represented by Bischoff in his view of the ovum of the dog, of which *fig.* 55 D. is a copy. I shall have occasion afterwards to state the nature of the fine canals which have been observed in the outer tunic of fishes' eggs.

It has been customary among ovologists, till very recently, to look upon the zona as corresponding to the external membrane of the yolk in the bird's egg. But from what has been already said in connection with that subject, the propriety of drawing a distinction between these two envelopes has been fully shown. I prefer, therefore, to retain the name of zona pellucida, though it may not be perhaps the best designation, as it prevents all confusion which might be introduced by views of its analogies. It will hereafter be more fully demonstrated that it not only differs in its mode of origin from the true vitelline membrane of birds, but that it also has a different destination in connection with embryonic development, inasmuch as, though formed in the ovary, it remains and constitutes the basis of, or becomes incorporated with, the important structure which at a later period becomes the chorion.

In the foregoing description of the membrane of the mammiferous ovum, I have adopted the view first advocated by Coste†, and by Thomas Wharton Jones‡; and more fully brought out and established by the researches of Bischoff in his admirable works on the development of the Rabbit and the Dog.§ It may be proper to remark farther, that though the name of zona pellucida has been employed to designate the thick single tough membrane by which, as is now well ascertained, the yolk of the mammiferous ovum is invariably enclosed from an early period of its formation in the ovary, this term is used synonymously with that of vitelline membrane, and as applied to

* Epistola de Ovi Mammalium et Hominis genesi, Lipsiæ, 1827.

* Müller's Archiv. &c. for 1854, p. 252.

† Recherches sur la Génération des Mammifères, 4to. Paris, 1834, fig. 2.; and Embryogénie Comparée, tom. i. p. 200, Paris, 1837.

‡ In a paper read to the Royal Society of London in 1835; printed in the London Medical Gazette for 1838, p. 680.

§ Entwickelungsgeschichte des Kaninchencies, Braunschweig, 4to. 1842; and Entwickelungsg. des Hundeies, Braunschweig, 4to. 1845.

the only covering with which the ovarian ovum is provided at the time of its leaving the Graafian vesicle, excepting that which it retains for a time derived from the cells of the tunica granulosa in the proligerous disc. Von Baer indeed, from whose description the term pellucid area or zone has been borrowed, was not fully aware of its consisting only of one thick membrane; and more than once, both in the Epistola and in the Commentary upon it, expresses himself doubtfully as to whether this pellucid space or halo* might not be formed of an external envelope which he terms the cortical membrane, and of another situated within it.

It is well known that when the mammiferous ovum has been fecundated, and arrives in the cavity of the uterus, and begins then rapidly to expand, it is covered by a membrane which soon undergoes great extension, and acquires a villous structure on its external surface, by which it may always be easily recognised. This villous envelope of the uterine ovum, universally now known as the chorion, is the product no doubt of changes which only occur in their completeness after fecundation, and as an accompaniment of embryonic development; but still as it appears probable that the zona pellucida is intimately connected with the first condition of the chorion, and as the first formation of the latter membrane is by many believed to take place independently of fecundation or fœtal development, it is necessary for me to make some remarks in this place on the relations of the zona pellucida to the external covering which the ovum obtains in the first periods of its residence within the female passages. This is a subject on which embryological writers are by no means agreed, and several of them indeed have themselves changed their opinions in regard to it in the progress of their researches.

Von Baer, the correctness of whose general views on the phenomena of development we have occasion to admire in almost every part of the subject of which he has treated, was at first of opinion that the chorion might arise in Mammalia from the outer of the two layers of which he at that time (though also doubtingly) conceived the external covering of the ovarian ovum to consist, and he looked upon this as a great difference or departure from analogy between the bird's egg and the ovum of the mammifer: but in his work on Development†, published eight years later than the Epistola and Commentary, he states his conviction from his observations, that in some mammiferous animals at least, such as the pig and sheep, the chorion is formed by external deposit on the surface of the ovarian ovum during its descent into the uterus, and therefore takes its origin more in analogy with the external covering of the bird's egg. At the same time he confesses that he was not able to reconcile this view with what he had seen in the dog and rabbit.

Valentin, in his Manual of the History of Development*, regarded it as most probable that the chorion is formed by the deposition and consolidation of an albuminous matter on the surface of the ovum during its descent through the first part of the Fallopian tubes; but though taking, as it appears, a perfectly correct view of this subject, he did not bring forward observations sufficient to establish the opinion which he had founded chiefly on analogical considerations.

We owe to Thomas Wharton Jones the first direct observation of the actual deposit of a layer of albuminous matter round the surface of the zona pellucida. But although Mr. Jones, in the observation which he made on the ovum of the rabbit within the Fallopian tubes on the third day after conception, was quite assured that a new structure had made its appearance in considerable thickness on the surface of the zona, yet he at first supposed that this might proceed from some change in the remains of the granular tunic which adhered to that membrane after it had left the Graafian follicle.† He afterwards, however, became aware of the source of this fallacy, and adopted the view that the mammiferous ovum receives a superadded structure, contributing to the formation of the chorion, in its descent through the tubes.

In the first series of his Embryological Researches, Martin Barry described not only the zona pellucida as recognised by other observers, but also a distinct vitelline membrane within it; and he conceived that the zona became afterwards the chorion. But in his second series he became aware, both from the statements of Wharton Jones and from his own observations, that a new deposit occurs in the rabbit's ovum; and this new deposit he now regarded as "the true chorion." He retained, however, for a time his view of the separate existence of a vitelline membrane; and thus described articulately three membranes as belonging to the mammiferous ovum, viz., vitelline membrane, zona pellucida, and chorion.‡ The first membrane he believed to disappear previous to the period of full maturity: the two last he regarded as together the source of the chorion of a later stage.

Bischoff also had not been aware from his earliest observations that any new deposit occurred round the ovum of the rabbit in the tubes; and even after he had become acquainted with this fact, and had observed it himself, as he did not detect a similar deposit on the ovum of the dog, he adhered to the

* Spatium pellucidum, halo vel peripheria lucida. See Commentary on the Epistola, as translated by Breschet in his Repertoire, 1828, p. 52.

† Beobachtung. und Reflexion. über Entwickelungsgesch. &c., Königsberg, 1837, part ii. p. 185.

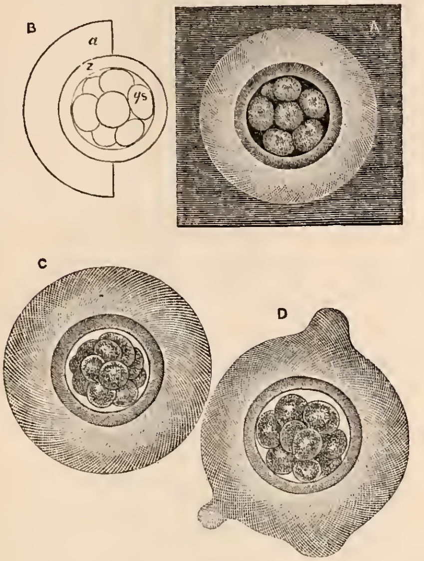
* Handbuch der Entwick. &c. des Menschen, Berlin, 1835, pp. 38, 39.

† On the First Changes in the Ova of the Mammifera, in consequence of Impregnation, and on the Mode of Origin of the Chorion, in Phil. Trans. 1837, part. ii. p. 339.

‡ See Phil. Trans. for 1839, p. 316.

view which he had previously taken, that the zona becomes the chorion, or at least that a new deposit is not in all Mammalia necessary for the formation of that membrane.

Fig. 57*.



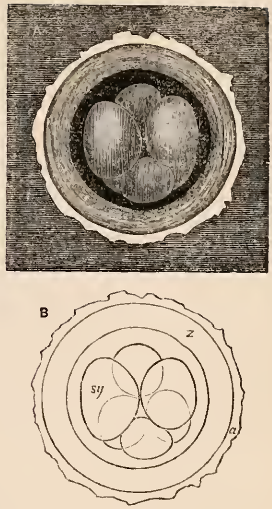
Ova of the Rabbit from the Fallopian tube three days after impregnation.

A, shows on a dark ground one of these ova, of which B is an explanatory outline. *y, s*, are the yolk segments of which there were eight; *z*, the zona; *a*, the thick layer of albumen which in this animal is always deposited on the exterior of the zona after the granular cells have been removed from it.

C and D. Other ova from the same animal; in D, are shown three projections of the albuminous covering which have been taken for villi of the chorion; but which according to Bischoff are not so. This ovum was farthest down in the Fallopian tube.

In a series of observations made by myself on the ovum of the dog and rabbit during their descent from the ovary to the uterus, in the summer of 1840, I was induced to adopt the opinion that a new deposit does really occur on the surface of the ovum in both of these animals. I repeatedly observed the large gelatinous or firm thick albuminous covering on the rabbit's ovum when it had just entered the cavity of the uterus; and in several instances I thought I could perceive the first formation of the villi of the chorion by sprouting or budding from the surface of the newly deposited substance, which, as in Wharton Jones' and Barry's observations, it was quite easy to distinguish from the membrane of the zona. In the ovum of the dog I admit, with Bischoff, the appearance is very different; but yet my observations appeared to me to demonstrate that in that animal also a substance is superadded to the surface of the zona, for that membrane, which presents at an earlier period a

Fig. 58*.



Ovum of the Dog from the Fallopian tube ten days after impregnation.

A. The yolk has undergone division into eight segments, and there is a thin irregular deposit of albumen on the outer surface of the zona. (This is represented too light in the figure.)

B. Explanatory outline of the same; *y, s*, yolk segments; *z*, zona pellucida; *a*, layer of albumen, from which in connection with the zona the chorion takes its origin.

perfectly distinct and smooth outline on its external surface, becomes in the course of the descent through the Fallopian tubes and by the time of its first arrival in the uterus, not only irregularly flocculent on its surface, but also thickened; in fact, presents all the appearance of a granulo-mucous substance having been deposited upon it.

It may be proper to explain here, that it has now been fully shown by Bischoff's excellent observations, that in both the animals mentioned, and also in the guinea-pig, the cells of the tunica granulosa, which adhere to the surface of the zona when it leaves the Graafian follicle, are completely separated from it within the first two or three days of the residence of the ovum within the tube, so as to leave the external surface of the zona perfectly smooth. Bischoff has shown, indeed, as I have also repeatedly observed, that a change has occurred in the cells of the proligerous disc, adherent to the ovum while it is still within the ovary, which indicates its approaching maturity. This change consists, as already stated, in these cells becoming somewhat spindle-shaped or pyriform, their narrow or pointed ends being attached to and radiating from the surface of the zona. (See as before *fig.* 55. D.) It is quite easy, therefore, after this separation takes place, to distinguish any change by addition of new matter or otherwise which the surface of the zona may undergo. No one can fail to perceive the addition to the ovum of the rabbit, the diameter of which is thus increased between two and three times, so as to give it somewhat the aspect of the ovum of a Batrachian in miniature; and in the dog it has appeared to me that the increased thickness and more opaque and flocculent roughness of the surface of the zona were sufficient proofs of a new deposit having taken place. This deposit, no doubt, becomes very completely incorporated with the substance of the zona, and is not easily to be distinguished from it; but in one or two instances I have thought that I was able to perceive a line of demarcation between them. Several of Bischoff's very faithful figures seem to me even to represent this deposit as it has occurred on the ova of the dog. But his statements in his work on the Development of the Guinea-Pig * are so precise against the occurrence of such a deposit, that further observations will be required fully to determine the question whether it is of constant occurrence or essential to the formation of the chorion.

Later observations lead me to think that I may have been in error in supposing that the villi of the chorion grow directly from the albuminous deposit. These villi, which, as I have said, form a most characteristic feature of the external covering of the mammiferous ovum in the course of development, begin to be formed only when the ovum has reached the cavity of the uterus. The time of the formation of these villi, as well as their size, varies, however, considerably in different animals, and probably also to some extent in the same animal.† They are developed from the external surface, and their structure is at first nearly homogeneous, or at least only slightly granular; they afterwards acquire a cellular structure, and in the course of fœtal development become at an early period the seat of a complicated vascular growth, by which the relations of the maternal parent and offspring are maintained through utero-gestation. But the fuller description of this part of the growth of the chorion belongs rather to the history of development after fecundation. My present object has been only to show the relation of this membrane to the zona or ovarian coverings of the ovum.

The contents of the ovum or parts within the zona consist of the yolk-mass or yolk-substance, and the germinal vesicle. The first of these constitutes a spherical mass of variable consistence, in which granules, or molecules and globules of various sizes, from the most minute up to about $\frac{1}{6000}$ or $\frac{1}{4000}''$, are suspended in a fluid. The proportion of the granules to the fluid varies to a considerable extent in different animals, the ovum being much more opaque, and usually of a dull-yellow colour when the granules are in large quantity, as is the case in most Carnivora, and may be easily seen in the dog or cat. The clear fluid in

* Entwickelungsg. des Meerschweinchens, 4to. Giessen, 1852.

† Barry and Bischoff.

Fig. 59*.

Ovarian ovum of the Rabbit. (*From Coste.*)

a, ovarian ovum extracted from a nearly ripe Graafian follicle, and freed from the adherent granular cells; the close set granules of the yolk substance, among which the germinal vesicle is perceived with a slightly oval macula or nucleus, are well represented.

b, the same burst by pressure; the yolk granules adhering together by a viscid clearer fluid substance are seen escaping from the large aperture in the zona along with the germinal vesicle.

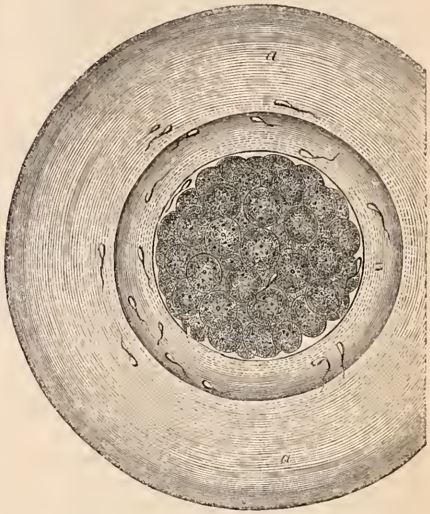
which the granules are suspended varies also in its consistence, being of a marked viscid quality in some instances, and thin and limpid in others; so that in some animals, when the zona is punctured, the yolk-substance flows freely out, while in others, and this is the case in the human ovum, the yolk-substance holds together as one consistent mass. The yolk-substance does not adhere in the slightest to the interior of the the zona, but on the contrary is readily detached from it; and in some instances, in the entire unimpregnated ovum, a space is seen between the yolk-substance and the zona, formed apparently by the imbibition of water between them. This separation between the yolk-substance and zona appears to be, at a later period, a constant and probably important change in connection with fecundation and development.

The granules of the yolk-substance are generally rather more densely set together and more firmly united towards the external surface. This circumstance has given rise to the belief among some observers in the existence of an additional delicate membrane enclosing the yolk-mass; but the most attentive observation by Bischoff, Wharton Jones, myself, and others has failed to detect such a membrane; and there is reason to think that the confident belief in its existence has had its origin in part at least in a desire to establish a more complete analogy between the ovum of birds and Mammalia, and to find accordingly a vitelline membrane as well as a chorion present in the ova of the latter.

The germinal vesicle is usually about a sixth of the diameter of the whole ovum; but it is sometimes larger, or between a fifth and a fourth. It possesses a delicate membranous wall of a spherical or spheroidal form and homogeneous structure: it is barely possible to observe the double line of the thickness of this wall with the quarter of an inch lens in the microscope. In most animals the germinal vesicle is readily distinguishable from the rest of the ovum by its superior clearness, excepting in those instances in which it is hidden by the great opacity of the yolk-substance; but then it may generally be made manifest by flattening the ovum by compression between plates of glass. The fluid which fills its cavity, which is generally very clear, contains some minute granules in suspension; and besides these there is apparent within it the macula germinativa or germinal nucleus. This last, which is in general well defined in the mammiferous ovum, varies slightly in different animals: in some presenting the appearance of a round globule, with a delicate circumscribing line almost amounting to a vesicular covering; but more frequently it consists only of a small spherical or discoid mass of fine granules. In a germinal vesicle of $\frac{1}{600}''$ in diameter, such as that of the rabbit, the diameter of the macula is about one-fourth of that of the vesicle, or $\frac{1}{2400}''$.

In the earlier stages of formation of the ovum the germinal vesicle is of smaller size; but it is then proportionally larger than the other parts. It is the part of the ovum first formed; the yolk-substance, which is subsequently deposited in gradually increasing quantity round it, together with the zona, grow at a more rapid rate than the vesicle, and thus the latter remains in the mature state proportionally smaller. As the yolk-substance is at first deposited nearly in equal quantity on every side of the vesicle, it for a time contains the vesicle in its centre; but as the formation of the ovum proceeds the vesicle is found in general to have approached the surface at one side of the yolk-substance; and in the mature ovum the vesicle seems to be imbedded in the most compact and superficial layer of fine granules of the yolk-substance. This place no doubt corresponds in Mammalia, as has been ascertained in Batrachia, to the point from which after fecundation the first cleavage of the yolk proceeds; but this fact has not yet been determined by observation in the Mammalia, nor has any one as yet succeeded in observing a canal or pore leading from the surface of the yolk-substance towards the germinal vesicle in the mammiferous ovum.

Fig. 60*.



Ovum of the Rabbit from the Fallopian tube with spermatozoa.

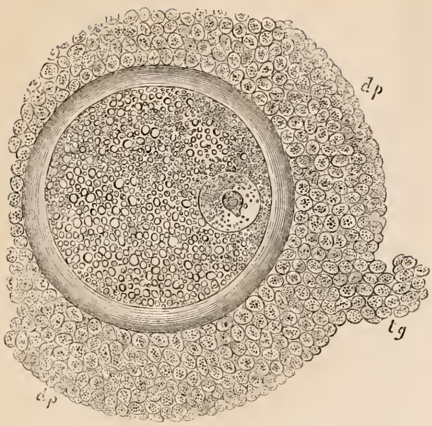
The accompanying figure is introduced to show the usual position of the spermatozoa in relation to the zona and albuminous layer in the ovum of Mammalia during and after impregnation. This ovum is magnified 250 diameters. It was taken along with five others from the lower part of the Fallopian tube 68 or 70 hours after impregnation. The segmentation appears to have proceeded to the fifth stage. There is a thick covering of albumen over the zona, and a number of spermatozoa are represented involved in the albuminous substance; some were also seen on the surface of the zona, and some, varying in number in the different ova observed from five to seven or nine, were clearly ascertained to be situated within the zona on the surface of and in the grooves between the yolk segments. The position of these last is not sufficiently clearly represented in the figure.

In the situation now described the germinal vesicle, though not by any means firmly fixed, is yet sufficiently embraced by the yolk-substance to prevent it from changing place when the ovum is moved in different directions. In the instances of the more fluid condition of the yolk it flows freely out from within the zona when this has been broken; but in those ova in which the yolk-substance is more viscid, as in the human ovum, we generally fail to isolate the vesicle from the rest of the substance.

The macula or nucleus appears to be attached to the inner surface of the membrane of the germinal vesicle. This is especially seen to be the case in the Pig, in which the macula seems to be somewhat pyriform or pediculated (see *fig.* 61*).

No important changes have been observed

Fig. 61 *.



Ovarian ovum of the Sow.

This ovum is represented in order to show the peculiar pyriform shape of the macula in the germinal vesicle, to the wall of which the macula appears to be attached. This ovum was taken from a Graafian follicle of $\frac{1}{12}''$ in diameter. The following are the dimensions of its several parts which are magnified 250 diameters in the figure. The ovum across the exterior of the zona $\frac{1}{175}''$; the vitellus $\frac{1}{200}''$; the germinal vesicle $\frac{1}{750}''$; the macula $\frac{1}{2100}''$; thickness of the zona $\frac{1}{2400}''$. The ovum is surrounded by the thick layer of cells which form the granular disc, *dp*. A few cells of the thinner membrana granulosa are represented at *tg*.

to occur in the germinal vesicle during the ovarian existence of the ovum. It usually disappears in Mammalia previous to the escape of the ovum from the Graafian follicle; but in this class of animals the phenomena attending the disappearance have not yet been fully investigated. There are some grounds for believing that immediately previous to the bursting of the vesicle there may be changes of the macula and other contents of the vesicle of a corresponding nature with those which have been more clearly observed in Batrachia and Fishes. Dr. Martin Barry seems to have observed something of this kind, and M. Coste has figured, but not so far as I am aware described, the development of cells in the germinal vesicle of a ripe ovarian human ovum.*

R. Wagner states, that occasionally a double macula may be seen in the germinal vesicle.† I have on one occasion observed two germinal vesicles within the same ovum in the dog.

Bischoff has on three occasions observed two ovules in the same Graafian follicle of the rabbit.‡ This had been previously noticed by Von Baer in the dog and pig. And Bidder § detected two ovules embedded in the same granular membrane of one Graafian vesicle of the cow. Upon the question how far these varieties in the structure of the ovum may be supposed to be related to the origin of Double-monsters and Twins, I must refer to Professor Vrolik's interesting article Teratology.*

For the assistance of those who may wish to engage in researches of the same nature as those by which the above facts have been ascertained, I will state shortly the manner in which the ova of Mammalia may be procured either from the ovary or after they have left that organ. 1st. For the examination of the earlier ovarian ova and follicles, thin sections of the ovarian substance are to be made, especially towards the surface of the ovary; and some of these are to be teased out with needle points, and examined with the aid of compression, &c. 2nd. For the more mature ovarian ovum, &c., the outer covering of the ovary is to be removed from the surface of one or more of the prominent follicles; and the latter may then, if large, be carefully dissected out of the ovary, and laid on a glass plate, where it is to be opened with a sharp-pointed knife, and its contents are to be gently pressed out on the glass. The ovum may in general be easily detected in a part of the tunica granulosa with a low magnifying lens, or even sometimes with the naked eye. In the ovary of the dog the ovum may sometimes be seen without any dissection towards the most prominent part of the surface of the mature follicles.† 3rd. To procure the ova after they have left the ovary, or while they are in the tubes, two methods may be pursued: either the whole length of the tube may be opened with very finely-pointed and sharp scissors, and the surface then spread out and examined carefully with a low magnifying power under a good elumination, but this must not be done under water; or another plan may be followed according to the recommendation of Martin Barry, founded on a suggestion thrown out by Cruickshank, as follows: The Fallopian tubes being divided into several portions, the contents of each portion are to be separately pressed out by passing a blunt instrument firmly along the outside of the tube, and, being placed on suitable plates of glass, are to be subjected to the necessary examination. The latter method is particularly convenient in small animals: in the larger I have followed both plans. The method of Barry certainly saves much time and trouble, and is on the whole sure enough.‡ 4th. Of the plan for obtaining the ova from the uterus, when of considerable size, as it belongs rather to the history of development, I will only say here that the greatest caution is necessary in cutting through the walls of the uterus in different layers so as to

* See the plate in his great work marked "Mammifères; Homme." Pl. I. Fig. 6.

† See Prodromus Hist. Generationis, Fig. xxxi.

‡ Müller's Archiv. Jahrsbericht, p. 169.

§ Müller's Archiv. 1842, p. 86.

* Vol. iv. p. 973. Cyclopæd. of Anat. and Physiol.

† See Von Baer's Commentary on his Epistola, in Breschet's Répertoire, 1828, p. 38.

‡ See Barry's Second Series of Researches, &c., Phil. Trans. 1839, p. 366.

avoid injuring the ova, and that the examination must be made at first in the dry state.

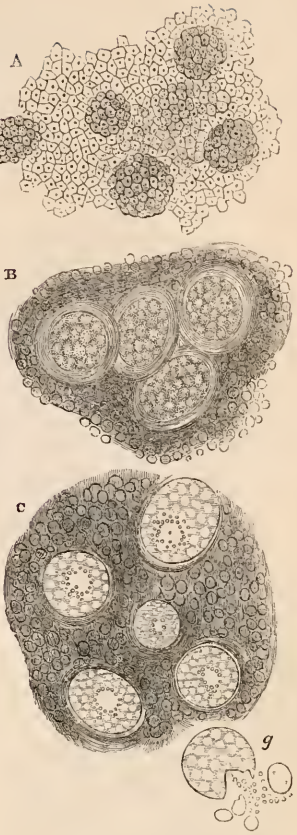
Origin and Formation of the Mammiferous Ovum.—This subject has already been adverted to in the previous section in connection with the history of the formation of the bird's egg. Dr. Martin Barry was led, by his numerous observations, to form the conclusion, that the germinal vesicle is the first part which makes its appearance in the ovarian stroma at the commencement of the formation of the ova. All observers seem now to be agreed, that of the parts belonging strictly to the ovum itself, the germinal vesicle is the first formed; but the observations of Valentin, Bischoff and others appear rather to support the view, which is opposed to that of Barry, that the Graafian follicles may be detected in the ovarian stroma before any part of the ovule is distinguishable.

The ovules are formed at a comparatively early period in the ovary. Carus was the first to point out * that in the ovary of the human female child the follicles containing distinct ovules are perceptible at birth. Vallisnieri had long previously, it appears, made a similar observation. Bischoff has, with more precision, pointed out, that there is considerable variation in different children of the same age as to the degree of advancement of the germs of ova within the ovarium; in some nothing more than a perfectly uniform ovarian stroma is perceptible at birth, while in others the follicles are distinctly formed, even at an earlier period. By the age of ten or eleven years a number of the vesicles are found to be approaching maturity, and almost all have left their earliest condition. Both Barry and Bischoff, however, are of opinion that new sets of Graafian follicles and ova may continue to arise within the ovaries during the whole child-bearing period of the human female; and there can be little doubt that this takes place in most of the lower animals.

Bischoff describes the Graafian follicles as taking their origin from minute heaps of granules in the ovarian stroma; but he has not been able to confirm the statement of Valentin that the earliest follicles proceed from primitive gland tubes stretching from the attached border towards the surface of the ovary.† In various animals the follicles and ova begin to be formed at an earlier period than in the human female: according to Bischoff, they arise very early both in the cow and pig.

When the primary follicle can be perceived, it consists of a small vesicle scarcely more than $\frac{1}{1000}''$ in diameter. To this primary vesicle Martin Barry has given the appropriate name of Ovisac. Soon afterwards, when the vesicle has expanded somewhat, it is found to contain the rudiment of the ovum; first in the shape of the very small germinal vesicle, generally surrounded by a small quantity of granular fluid. Soon afterwards the outer follicle is lined with a few extremely delicate or hyaline hemispherical cells, which have somewhat the appearance of those of epithelium, and which thus give rise to a clear space between

Fig. 62*.



Development of the Ovarian ovum of Mammalia. (*From Bischoff.*)

A represents a very small portion of the ovary of a fœtal dog. The commencing Graafian follicles are visible in the granular or cellular stroma of the ovary, constituting dark heaps of more opaque granules or small cells.

B, fragment of the ovary of a dog three weeks after birth. The Graafian follicles are now seen in the fibro-granular ovarian stroma, each surrounded by a homogeneous and fibrous covering, and filled with granules.

C, fragment of the ovary of a pig three weeks old. The Graafian follicles are now seen to be formed of a fine transparent vesicular membrane, and round the larger ones fibres are beginning to be deposited. The wall of the follicles are lined internally with delicate epithelial cells. The germinal vesicles now visible within consist of a fine clear cell with a nucleus or dot, and a few vitelline granules have begun to be deposited round the germinal vesicles.

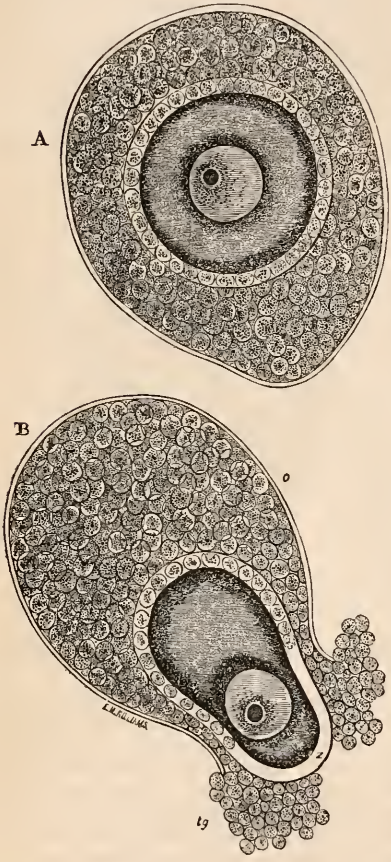
g, one of these Graafian follicles burst with a needle, showing the contents of the follicle; there being as yet no zona or vitelline membrane.

* Müller's Archiv. for 1832, p. 379.

† Handbuch der Entwickelungsgeschichte, 1835, p. 389.; and Müller's Archiv for 1838, p. 529.

the membrane or wall of the follicle, and all that yet exists of the ovule. Next, the yolk substance is formed round the germinal vesicle; first of all, as has been shown by Leuckart†, by the deposit of a clear viscid fluid, and next by the formation of dark or opaque small granules in this fluid adjacent to the germinal vesicle. Somewhat later the zona pellucida,

Fig. 63*.



Ovarian follicle and ovum of the Rabbit at an early stage.

The follicle here represented was about $\frac{1}{100}$'' in diameter: in the figure it is shown as it appears under slight pressure. All the parts of the ovum are distinct, and its large size in proportion to the follicle and tunica granulosa is apparent. In the lower of the two figures the follicle is represented as having been burst by pressure and the ovum with the tunica granulosa in the act of escaping from within: the yielding character and elasticity of the zona is shown by the change of form during the escape, and the ovum afterwards regaining its spherical shape. *o*, the wall of the follicle; *t g*, the tunica granulosa; *z*, the zona partially freed from the cell covering. The macula with the germinal vesicle is remarkably distinct, and is surrounded by a quantity of fine molecular substance.

† Article Zeugung in Wagner's Handworterbuch der Physiologie, 1853.

which cannot be said to have existed from the first, comes to be apparent outside the opaque granular substance of the yolk, and close to the epithelial cells which line the follicle: it seems as if it owed its origin to the condensation of the outermost layer of the clear basement matter from which the yolk-substance is formed.

The membrana granulosa consists for a time of a single layer of nucleated epithelial cells situated between the ovule and the Graafian follicle. The latter not being yet expanded by fluid, is at this period completely filled by the ovum. Such is the state of the parts, now all present, in follicles of from $\frac{1}{100}$ to $\frac{1}{200}$'' in diameter. Subsequently the follicle increases in size much more rapidly than the ovum; the membrana granulosa follows closely the wall of the follicle in its rapid expansion by the increasing accumulation of fluid within; and the ovum is now found to be imbedded in a particular portion of the layer of granular cells constituting the *cumulus*.

According to the best observations, then, as to the formation of the mammiferous ovum, it appears that the ovarian follicle, which we may look upon as the primary gland cell, is first produced; that within it at a very early period the germinal vesicle with its nucleus next arises, and that very soon after the origin of this primary part the yolk-substance commences by a deposit of fluid and granules round the germinal vesicle; that the Graafian follicle is lined by a layer of nucleated cells resembling epithelium, which constitute the commencement of the tunica granulosa; that the zona pellucida, which forms the outermost covering of the ovum when it leaves the ovary, is formed at an early period, but somewhat later than the commencement of the other parts of the ovum; and that it probably owes its origin to a membranous condensation of the outermost part of the clear primitive yolk-substance; and that, finally, the tunica granulosa increases in quantity and extent, is expanded along with the follicle by the fluid within it, and being deposited at its thickened cumulus round the ovum encloses it in a part of its substance.

The structure of the ovum is, on the whole, very similar throughout all the families of the class Mammalia in which it has been examined, excepting one, viz., the Monotremata. In Marsupialia, in which, from the remarkable deviation from the more common mode of gestation, it has been supposed that the ovum might present some peculiarities, it does not appear, from the observations of Professor Owen, that any remarkable difference is to be detected. In the ovisac there was observed a somewhat larger quantity of granular substance than usual; but the diameter of one of the largest ova in the *Macropus Parryi* or Kangaroo was not greater than $\frac{1}{120}$'', and the germinal vesicle was only $\frac{1}{1680}$'', which is proportionally small; so that it cannot be held that in this animal there was apparent any approach to the oviparous type.

In the Monotremata, however, the ovum is of much larger size, and appears to occupy the whole or the greater part of the ovarian follicle or capsule; more in the manner of that in birds and scaly reptiles. According to Professor Owen*, the ovaries of the Ornithorhynchus present numerous elevations on their surface caused by the projection of ovisacs of different sizes and in different stages of development. The largest of these sacs have a diameter of two lines; and, as in birds, though in a less marked manner, the right oviduct and ovary are less developed than the left. The unimpregnated ovum nearly completely fills the ovisac or ovarian capsule. The germinal vesicle is of a comparatively large size, being about $\frac{1}{250}''$ in diameter. The vitelline substance is rich in nucleated (?) cells or granules, intermixed with clear colourless oil globules. The vitelline membrane is moderately thick and smooth, and refracts light strongly. The ovum is separated from the inner surface of the ovarian capsule by a very small quantity of fluid, and by a stratum of granules or cells.

The ova found in the uterus of the Ornithorhynchus were of a deep-yellow colour, with a smooth polished surface, and had no adhesion to the inner uterine membrane. In one animal the yolks were found enclosed in a more transparent mass, which was surrounded by a cortical membrane of some tenacity, presenting in fact some resemblance to the albumen and shell membrane of a bird's egg. Leuckart † thinks it probable that Owen may have been misled as to the size of the ova by the examination of specimens which had been preserved in alcohol; but Professor Owen informs me, that he was fully on his guard against such an error, and was quite satisfied of the approach in the structure of these ova to the oviparous type of birds and reptiles.

I have examined the ovaries in a specimen of *Echidna hystrix*, which has been preserved in alcohol; and although the somewhat deteriorated state of the specimen, and the circumstance of the ovaries not being in the fully developed condition, were not the most favourable for minute observation, I was convinced that the ovarian ova of this animal, like those of its congener the Ornithorhynchus, belong rather to the oviparous than to the usual mammiferous type. The yolks, which quite filled the ovisacs, were some of them about $\frac{1}{20}''$ in diameter: they contained a large quantity of granular globules similar to the yolk corpuscles of birds; the yolk, in fact, consisted of the nutritive as well as the formative substance; and the whole aspect of the ovary, as well as of the individual yolks, recalled to my mind that of an oviparous animal in a somewhat undeveloped state.

* See Prof. Owen's Article Monotremata in this Cyclopædia, and his Memoirs in the Philos. Trans. for 1832 and 1835. See in particular figures 191, 192, and 194 of the article Monotremata, Cylopæd. of Anat. vol. iii. p. 393, et seq.

† Article Zeugung, p. 783.

The ova of a considerable number of the Invertebrate animals belong to the same group under which I have placed that of Mammalia; that is, they consist principally of formative or granular yolk-substance, undergo complete segmentation, and have a simple zona or structureless covering; but yet the varieties in structure, relations, and mode of production among these ova themselves, and their differences from the ova of Mammalia are so great, that I think it will conduce to greater clearness and prevent repetition, to defer treating of the ova of Invertebrata till after I shall have given the description of the remaining ova of the Vertebrate animals, to which we shall now proceed.

Third Group of the Ova of Vertebrate Animals.—Under this head I have now to state some details as to the structure, relations, and mode of formation of the ova of amphibious reptiles or chiefly the Batrachia, and of osseous fishes. The ova of both of these tribes of animals appear to occupy an intermediate place between the very small and granular-yolked ova of the Mammalia and the large cellular-yolked ova of birds and scaly reptiles. They agree in both possessing a yolk of moderate size, in the substance of the yolk being principally or largely of the formative kind, and in the possession of a proportionally large germinal vesicle, in which the macula is not a single nucleus, but rather a large collection of nuclei or maculæ. In both of them the segmentation is partial or not complete, affecting chiefly the superficial part of the yolk, in which the formative or germinal portion of the yolk is placed, but varying considerably in the depth and the extent of the surface which it involves in different species and genera, more especially among the Amphibia. In the predominance of the formative yolk and in its relations to the process of segmentation, therefore, they approach the Mammalia, while in the large size and structure of the germinal vesicle in all, and in the considerable amount of nutritive yolk in some, they more nearly resemble the group of large-yolked ova. It will be proper, on account of the differences between them, to describe separately the ova of Amphibia and those of Osseous fishes.

Amphibia.—Batrachia.—The ripe ovarian ovum of the common frog or toad is a nearly spherical body of from $\frac{1}{15}$ to $\frac{1}{12}$ of an inch in diameter, of a dark colour, contained within and closely embraced by a thin vascular sac formed by the dilatation of the ovisacs which hang into the general ovarian cavity.

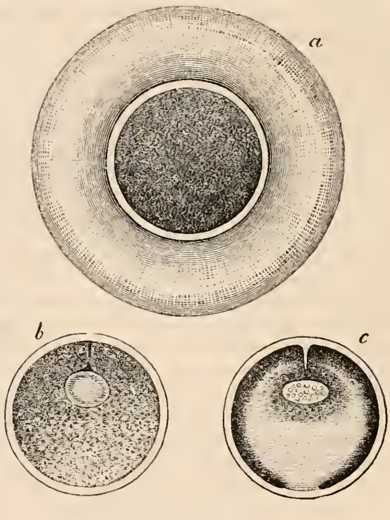
This capsule or ovisac is attached to the rest of the ovarian substance by a broad band rather than by a narrow pedicle; and when the yolk or ovarian ovum is mature, it escapes from the ovisac by the formation of an aperture in the remote or free side of this capsule, somewhat in the same manner as occurs in the calyces of the bird, but with a wider aperture. Through the apertures of the general ovarian capsule the numerous ova pass into the abdominal cavity, during the first period of sexual union, and they are thence taken up singly by the open upper extremities of the two oviducts ; through the whole of which canals they descend, and in their passage receive an additional covering of a peculiar gelatinous or albuminous substance, which adheres closely to the surface of the yolk membrane, and is firm and of comparatively little bulk while the ova are still within the oviduct, but which after exclusion rapidly swells by the imbibition of a large quantity of water, so as to become several times its original thickness, and to assume a soft gelatinous consistence.

The ova which have passed through the oviducts remain for a time accumulated in large numbers in a dilated part of the canals near their lower end, until the whole or greater part of those which are ready to descend from the ovary have passed down ; and then, while the male still continues united with the female, the ova are rapidly excluded, and the male sheds the spermatic fluid in abundance, partly on the ova as they pass into the water, and partly after separating from the female, upon the spawn as it floats in the water. The importance of the imbibition of water by the gelatinous covering immediately on the exclusion of the ova and just at the time when the spermatic fluid has been placed upon them, in securing the access of the spermatozoa to the surface of the vitelline membrane through the stiff jelly, and in thus promoting fecundation, will be afterwards more particularly adverted to.

In the tailed Amphibia, such as the different kinds of Newt (Salamandra, Triton, and Lissotriton) there is not the same union of the male and female as in the tailless or Anurous Batrachia ; and impregnation takes place by the entrance of the spermatic fluid, shed in the water by the male while placed near the female, into the oviducts of the latter. In these animals the external covering consists of an elliptical membranous capsule filled with a clear fluid and containing the coloured spherical yolk ; but there is also externally a small quantity of gelatinous substance which in some of them serves to attach the ova to leaves of plants or other objects. In the common larger and smaller newts the ova are in smaller number than in the frog or toad, and are excluded one by one by the female, which deposits them singly in a folded leaf or other place of security.*

The yolk of the ripe ovarian ovum in Amphibia consists of a thick opaque mass of vitelline substance, within which and towards one side the large germinal vesicle is placed. The vitelline substance is usually of a darker colour on the exterior and lighter in the centre. In the common toad the superficial part is almost black ; in the common frog, *Rana temporaria*, it is of a very dark brown ; and it is in different other species of various hues, as stated in a former part of this article. The dark superficial part does not in general cover the whole surface of the yolk, but is deficient on one side ; and its extent as compared with the inner paler part, which appears where the dark part terminates, varies in different species and is greater in proportion to the degree of advancement of the ova. In some species, as in the *Alytes obstetricans*, of which C. Vogt has given an excellent description†, it does not, when the ovum is mature, occupy more than a half of the surface ; but in the common frog and toad it covers so much of the surface of the yolk when it is about to leave the ovary, that the gray internal part is only seen as a defined round spot on the opposite side. In the undeveloped ovarian ova, however, the dark part is much more limited in its extent, thus allowing a greater part of the lighter-coloured internal part to be seen.

Fig. 64 *.



Ovum of the Frog.

a. (*From Newport.*) An ovum of the frog half an hour after impregnation, covered with its gelatinous mass. The dark part of the egg or yolk is seen to be surrounded by a vitelline membrane. Spermatozoa were seen everywhere in the gelatinous envelope, but are not represented in the figure.

b. Vertical section of the yolk or ovarian ovum of the frog which has been hardened in alcohol, showing the germinal vesicle within and the canal of the yolk which leads down to it from the upper or germinal pole. The external line indicates the vitelline membrane.

c. Diagrammatic representation of the same section, showing, according to the views of Ransom, the relation of the canal or depression of the yolk to the germinal vesicle. The micropyle, if it exists in these ova, may be situated in the vitelline membrane immediately above this canal. This figure also shows the relations of the dark and light coloured parts of the yolk substance.

* I have frequently observed this process, which has been beautifully described and figured by Mauro Rusconi in his work, "Amours des Salamandres Aquatiques, Milan, 1821."

† Entwickelungsg. der Geburtshoelferkröte, Solothurn, 1842.

It is towards the centre of the dark superficial part of the yolk that the first changes of embryonic development always take place; and it is apparent that this dark part corresponds more immediately to the germinal part of the yolk. It is beneath the central part of this dark covering that the germinal vesicle is situated in the ripe ovum. When taken from the ovary previous to impregnation, the ova float in water indifferently as regards the position of their parts; but after impregnation, when the imbibition of water allows of the free rotation of the yolk within its coverings, it is invariably found that the dark or germinal part of the yolk is directed upwards, and the whiter or grey spot downwards; — a circumstance by which the difference between the fecundated and the unfecundated ova may readily be detected. We may distinguish therefore, as the upper, dorsal, or germinal pole of the ovum, the central point of the dark part, and name the opposite point in the centre of the light-coloured space the lower or ventral pole.

The thickness of the dark layer of substance which covers the upper part of the ovum is throughout its greater part considerable; viz. about one-eighth to one-tenth of the whole diameter of the yolk. It thins off somewhat at its edges below. Within this darkest layer the colour of the yolk-substance is slightly shaded off into the grey substance of the interior: the consistence of the inner substance is less than that of the superficial layer, and it contains a cavity situated considerably nearer the upper than the lower surface of the yolk, in which the germinal vesicle is situated. This vesicle is not perfectly spherical in its form, but somewhat flattened from above downwards, and it is surrounded by a peculiar mass of fine granules.

The yolk-substance contains no cells nor large corpuscles; the greater part of it consists in the mature state of peculiar flat or tabular corpuscles, the largest of which are about $\frac{1}{2500}''$ in diameter. Most of these are quadrangular in shape, but somewhat rounded on the edges and at their angles. There are also numerous smaller particles of the same kind of every dimension from that already stated down to the smallest granules, and with some variation of shape, together with a considerable amount of molecules of very minute size, of which those in the darker part have the appearance of pigment granules. These last are accumulated in greatest quantity towards the surface; but they do not constitute a separate layer, being rather interspersed with the tabular corpuscles. There are also to be seen in the upper or germinal part a few rounded corpuscles, somewhat larger than the tabular particles, which seem to be formed by the aggregation of smaller molecules; but these have no external envelope nor clear nucleus, and only bear a distant resemblance to the cells which, after impregnation, are formed in the germinal part of the yolk-substance.

The peculiar quadrilateral tabular corpuscles refract light strongly, so as to present distinct outlines; they have also considerable firmness, resisting pressure, but by force may be broken up somewhat in the same manner as would occur in small plates of wax. From this circumstance they have generally been regarded as of a fatty nature, and were described by Vogt as stearine tables; but Virchow*, from a careful investigation of their reaction with different substances, throws a doubt upon this view, and is more inclined to regard these corpuscles, both in Batrachia and in the ovum of the carp-fish, as composed of some albuminous or protein principle, the exact nature of which he has been unable to determine. He admits that they may also contain some oil. They are probably very analogous to the larger firm angular particles which were first described by J. Müller as forming the greater part of the yolk-substance in the Sharks and Rays, and which also exist in the ova of Cephalopodous Mollusca.†

The germinal vesicle of the Batrachian ovum is of very large proportionate size. According to Vogt, in the *Alytes obstetricans* its diameter is nearly equal to one-third of that of the entire yolk mass. In the common frog and toad it is somewhat less, but nearly $\frac{1}{40}$ of an inch. This vesicle may be obtained separate for examination by breaking open the yolk carefully under water; but it is much easier to observe its position, form, and structure in the ovum which has been hardened by some re-agent,—a plan which has been successfully adopted by a variety of observers. Cramer‡ recommends for this purpose alcohol, or more particularly dilute chromic acid; Newport§ employed alcohol, as I also have done with success; more recently Remak|| states that he has found a mixture of a solution of sulphate of copper with alcohol, to which a few drops of rectified wood spirit are added, peculiarly fitted to give the proper consistence to the various parts, without inducing any destructive change in their structure or appearance. All observers agree that there is scarcely any other animal in which the relations of the germinal vesicle to the other parts of the yolk can be more favourably investigated.

The enclosing wall of the vesicle is of extreme tenuity, so thin, indeed, that some have doubted its existence. I have been able, however, to distinguish the double outline of its thickness with a good magnifying power of 350 diameters. The outer surface of the vesicle is not always of a regular circular or spherical form, but often presents within the yolk, both at earlier and more advanced stages, a notched

* Zeitsch. für Wissensch. Zool. vol. v. p. 241.

† See J. Müller, über die Glatten Hai des Aristoteles, 1842, p. 36.

‡ Bemerk. über das Zellenleben in der Entwick. des Fröscheies, in Müller's Archiv. 1848, p. 20.

§ Researches on the Impregnation of the Amphibia, First Series, in Phil. Trans. for 1851, p. 169. *et seq.*

|| Untersuch. über die Entwickel. der Wirbelthiere, Berlin, 1855, p. 127.

appearance: when, however, the vesicle has been extracted from the yolk, I have generally found this appearance to be removed and perfect sphericity restored. It would appear also, from Vogt's observations in Alytes, that this appearance is not constant: it may depend on the viscidity of the contents, and the extreme softness and thinness of the enclosing membrane of the vesicle.

It is only in the earliest stages of ovarian formation that any appearance of distinct maculæ, such as they have been described in other animals, is to be perceived; for from a very early period these spots or nuclei are already very numerous. As the ova approach maturity the contents of the germinal vesicle undergo very considerable and rapid changes, by which a number of corpuscles, some loose, others aggregated, and subsequently delicate cells, are formed, and completely fill the whole cavity of the vesicle.

The germinal vesicle is situated, in the ripe ovarian ovum, nearer the upper than the lower part of the yolk. When the egg has been hardened by the re-agents already referred to, there can be perceived in the middle of the upper surface, or exactly in the upper or germinal pole of the yolk, a minute depression, which was first noticed by Prevost and Dumas *, and which they, erroneously, according to most of the observers who have followed them, conceived to be connected with an aperture or pore in the external membranes of the ovum. Von Baer showed that this depression leads into a canal which extends from the upper pole of the yolk, through the yolk-substance, to the surface of the germinal vesicle. The existence of this canal has been fully established, and its situation well represented by Newport. The interval between the upper surface of the yolk and the germinal vesicle appears to become less as the ovum approaches maturity.

The vitelline membrane of the mature ovarian ovum in the frog is thin and homogeneous. In the ova which have escaped from the ovary into the abdominal cavity it is still so thin, that they are very liable to be broken by the slightest force applied unequally on their surface; but in their descent through the oviduct considerable consistence is given by the addition of the layers of albumen to the vitelline membrane. Besides the simple vitelline membrane, there appears to be a second envelope formed within the albuminous deposit. Remak †, indeed, describes the vitelline membrane itself as consisting of two layers, besides the superadded membrane within the albumen.

Formation of the Ovum, and Changes in its Progress. — The ovary of the Batrachia is peculiarly well adapted for making observations on the development of the ova, as the stroma is in small quantity and transparent, and as it contains at most seasons a considerable number of ova in different stages of their formation and progress. If examined in the autumn or in spring before pairing, there are generally found three sets of ova; one uniformly large and dark-coloured, obviously belonging to those which are about to be brought forth in the ensuing breeding season; another set, also of uniform size, but less than the first, and in which only a partial deposit of colouring matter has taken place, probably constitute the ova for the next season after the first; and, third, a number of ova of inferior magnitude to either of the other sets, and of most various sizes, down to the most minute, which we may suppose to comprise those destined for succeeding breeding seasons. It seems probable that three seasons are necessary for the full development of the ova in the common frog and toad.

The earliest ova are seen within the ovicapsules or ovisacs, in the delicate ovarian stroma; the more advanced are enclosed in their pediculated capsules or calyces.

The germinal vesicle is the part of the ovum first distinctly recognisable; but so soon as it, or any part of the ovum can be distinguished, the delicate membrane of the ovisac or ovarian follicle is also seen surrounding it. Leuckart * was never able to perceive a follicle without there being already also an ovum within it. It would appear, therefore, either that the follicle and germinal vesicle arise together, or that observations have not yet determined which of them has the priority. It has been stated by some, that in the very earliest periods a single macula or nucleus may be observed in the germinal vesicle †; but it is rare to find the germinal vesicle in this state, and I have generally observed the macula, even in the earliest stages, to be multiple, or to consist of several maculæ. Still it is undoubted that, in the earliest period, there are fewer maculæ than at more advanced periods, and that their number gradually increases. About the time of maturation of the ovum the contents of the germinal vesicle undergo further changes, to which reference will hereafter be made.

From a very early period, though perhaps not from the first, the germinal vesicle is surrounded by a thick viscid substance, which closely adheres to its surface. This substance is at first remarkably clear, especially at its outer part, where it has a hyaline appearance: a little later it becomes gradually more and more opaque, as if by the deposit in or mixture with its clearer substance of fine molecules or granules. This appears to be the primitive yolk-substance; which in these animals therefore, as in most others, is ascertained to consist of a clear basis or matrix, in which the granular part is suspended. The out-

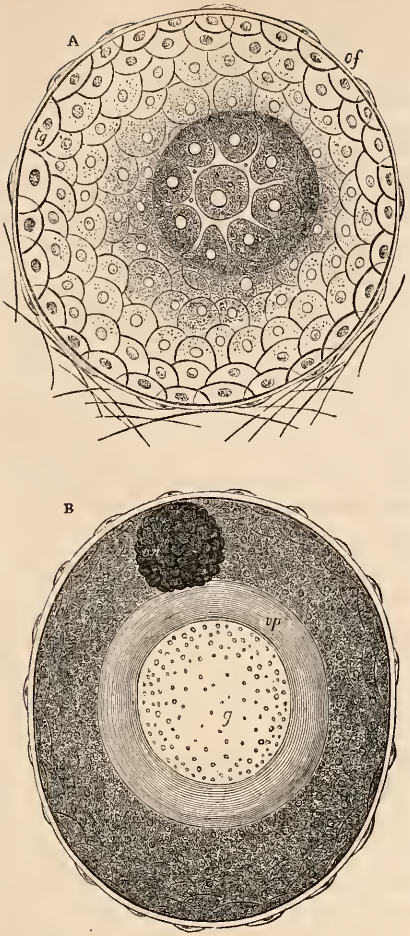
* 2me Mém. sur la Génération, &c., in Annal. des Scien. Nat. 1824, tom. ii. p. 104.

† Loc. cit. p. 127.

* Loc. cit.

† Mr. Newport describes the germinal vesicle of the frog's ovum as nucleated, even when half-grown. He also speaks of the corpuscles of the yolk substance as "nucleated cells" (1st Series, p. 176.); but this is quite inconsistent with the statements of most other observers.

Fig. 65 *.



Formation of the ovarian ovum in the Frog.

A, and B. Magnified representations of an ovarian follicle and its contents in an early stage of the formation of the ovum. The follicle is $\frac{1}{100}''$ in diameter: in A the follicular membrane and its epithelial lining are chiefly brought into focus; in B the parts of the ovum within are represented when the microscope was adjusted so as to place them in focus. The wall of the ovarian follicle consists of a structureless membrane or ovicapsule, and an external covering of thin flattened cells; the epithelial cells of the follicle within are seen in profile towards the margin, and full towards the centre (in A) where their granular contents and nuclei are distinct. In the centre of B the large germinal vesicle with numerous maculæ is seen; around it a clear space which is a part of the basement substance of the primitive yolk, and between this and the wall of the follicle there is seen superiorly the dark granular mass which has been called yolk nucleus. The clear primitive yolk is also surrounded by a finely granular vitelline substance which has begun to be deposited.

line of the clear part remains remarkably smooth and well-defined for a time, and there appears to be some fluid or different substance interposed between it and the inner surface of the ovicapsule. The homogeneous membrane of the latter is found at an early period to be lined by a single layer of very distinct largely nucleated cells, which lie flatly applied against its inner surface, but bulge or project roundly on their other sides towards the ovum. This layer of cells no doubt corresponds to the tunica granulosa of the ovisac in other animals, and has a similar destination.

There is as yet, neither in the earlier ova nor in those half-grown, any zona or other proper vitelline membrane; and it is obvious that what some authors* have described as such could be nothing more than the distinct surface of the primitive yolk. Whether this surface becomes condensed into a membrane, or at what time this may occur, has not yet been determined by observation.

Besides these parts in the early Batrachian ovum, there is another which has frequently been seen by various observers from Von Baer downwards, and which, as it is different from anything that has been observed in the ova of other Vertebrata, deserves some attention; I refer to a dark mass of granules situated excentrically or towards the side of the clear primitive yolk-substance, and between it and the tunica granulosa of the ovisac, and which, from its supposed connection with the formation of the yolk-substance, has been called the *yolk-nucleus*. This mass may easily be seen in ovisacs of the common frog of from $\frac{1}{150}$ to $\frac{1}{100}$ of an inch in diameter. It is then about one-tenth of the diameter of the ovisac. It is very opaque as compared with the other parts, being composed of aggregated heaps or small balls of finer granules. The opaque granules of the yolk have been supposed to be derived from this body, and it has been alleged that, as the yolk-substance increases, this yolk-nucleus gradually disappears or spreads itself round the germinal vesicle.† Leuckart, however, states that this body is not invariably present, and that it is subject to considerable varieties, and he is not inclined to attribute to it any important function in connection with the formation of parts of the ovum. I have in general found it present, and think it more probable that it may be destined to form the external and larger corpuscles of the yolk, while the clearer part immediately surrounding the germinal vesicle may contribute to the production both of these and of the finer substance in which the germinal vesicle is found imbedded. But farther observations will be required for the determination of these points.

As the growth of the ovarian ova proceeds, the deposit of fine granules in and around the primitive albuminous yolk-mass increases rapidly; and the yolk-nucleus, becoming less distinct, finally disappears at an early but somewhat variable period. The yolk-sub-

* As Cramer, loc. cit. p. 21.

‡ See V. Carus in Zeitsch. für Wissen. Zool. vol. ii. p. 103.; and Ecker in his new edition of R. Wagner's Icones Physiolog. descript. of Tab. xxiii.

stance contains at first only fine granules; but in the second season of development there are found mixed with these, especially towards the surface, corpuscles of a somewhat larger size, and these are gradually converted into the quadrilateral tabular particles. The distinction of colour between the surface and the deeper parts, and between the upper and lower portions of the yolk, also now appears; but it is not till the third season of development that, along with a proportional enlargement of the yolk, the darkest kind of pigment is deposited among the corpuscles on the upper surface. The gradual extension of this coloured layer over a greater portion of the surface of the yolk from the upper towards the lower part has already been stated. The extent of the coloured portion marks in fact, in a great measure, the proportion which the immediately germinal part of the yolk bears to that not concerned in the first process of embryonic development; or it indicates at least the extent of the yolk which is immediately involved in the process of segmentation.

The vitelline membrane, I have already said, is absent during the early stages of development of the ovum; it appears to be present in the third season, but I have not been able to determine precisely its mode of origin. Farther observations are still necessary to ascertain whether, as in Mammalia and some other animals, a zona is formed by the condensation of the outer part of the primitive yolk-substance, or whether this membrane proceeds from another source. From the gradual flattening and disappearance of the inner cells of the ovarian follicle, and the close adhesion of their remains to the vitelline membrane in the later stages, I am led to believe, that the covering with which the yolk leaves the ovary may owe its origin to the amalgamation of one or more layers of fused or united cells of the tunica granulosa, or to the union of these with the zona or primitive vitelline membrane, should such exist.

There is no true cellular yolk, but the granular yolk is of proportionally large size; and if we are disposed to regard the yolk as containing both a formative and nutritive part, these are united or combined in a more close manner than in the larger ova of ovipara. The ova of Batrachia differ, on the other hand, greatly from those of Mammalia in their relation to the Graafian follicle; more especially in the fact of the ovum completely filling the follicle, and the entire absence, excepting in the epithelial lining, of fluid or other deposit between that layer and the surface of the ovum. The history of development shows that the peculiar structure of the ovum of Batrachia, as well as that of osseous fishes, has some connection with the large proportion of the yolk which becomes immediately germinal, and with the comparatively early period of advancement at which the young leave the egg and assume an independent mode of life.

Before concluding this account of the ovum of the Amphibia, it will be proper to notice the changes that have been observed in the germinal vesicle near the time of the discharge of the ova, and in its descent through the tubes till its exclusion. All observers are agreed that the germinal vesicle is no longer visible in the excluded ovum, whether fecundation shall have occurred or not; and the solution or disappearance of this vesicle is now looked upon, in these as well as in other animals, as a natural concomitant of the maturation of the ovum independently of fecundation. The recent and very precise observations of Newport * have shown, that in a considerable number of the ova about to leave the ovary but still situated within that organ, the germinal vesicle has disappeared, and that it is invariably gone in all those which have passed into the abdominal cavity.

Very shortly before disappearing, and when the ovum is approaching maturity, a remarkable change has been observed in the contents of the germinal vesicle; which is of great interest, in consequence of its probable intimate relation to the process of segmentation and cell-formation, which follow fecundation and are the precursors of true embryonic development. These changes have been described first by Cramer, and afterwards by Newport; the latter author, apparently, not having been aware of the observations of the former.

In early spring (February) Cramer † found the fine granules into which the maculæ of the germinal vesicle had previously been resolved by multiplication, beginning to unite together into heaps or small masses; and somewhat later he found these masses to become surrounded by a fine membrane or envelope, giving them all the appearance of small cells with a granular nucleus. There are often several hundred such cells at this period in the germinal vesicle of the brown frog, varying slightly in size and shape. At a still later period the greater part of the granular nuclei or contents of these cells become dissolved, leaving only a few remaining in each; and finally these also disappear, so as to render the cells entirely clear.

Now, all observers are agreed, that in the yolk-substance of the ovarian ovum, previous to the rupture of the germinal vesicle, there are not to be perceived any other solid particles excepting those already mentioned, viz., granules or heaps of granules, and the peculiar quadrangular tables; but many observers have perceived that immediately after the disappearance of the germinal vesicle, and during the whole time previous to fecundation, as well as after that change, the yolk-substance contains, mixed with the darker corpuscles, other clearer and spherical vesicular globules, somewhat larger than the tabular corpuscles. Vogt described them as scattered through the whole of the superficial yolk-substance in the *Alytes obstetricans*, and Cramer pointed out that these vesicular corpuscles are identical with the cells which he had observed to be formed in the germinal vesicle immediately before its

* Researches, &c., 1st Series, p. 177.

† Müller's Archiv. 1848, p. 23.

disappearance. He attributed their origin, therefore, to this source; and regarded it as probable that these cells, which may perhaps be descendants of the original maculæ of the germinal vesicle (but this is a point which he leaves undetermined), constitute afterwards the nuclei round which the tabular and granular substance of the yolk group themselves; and thus probably form, subsequent to segmentation, the nuclei or foundation of the cells which are the seat of true embryonic development.

Newport's description of these changes differs somewhat from that of Cramer, but is not altogether at variance with the view now suggested as to the nature of the process with which they are connected. He states *, that towards the period of maturity he found the germinal vesicle filled with secondary cells, and that each of these contained other or tertiary cells within them, and in the interior of these last were granules which he called quaternary. "In the midst of these numerous cells, and in the centre of the germinal vesicle, I was able to distinguish," says he, "in some specimens, one or two cells of larger size than the rest, and which I regarded as the remains of the germinal spot or central nucleus." He further states †, that these internal cells were, he conceived, afterwards thrown loose by the solution of the parent cells.

As to the mode of disappearance of the germinal vesicle, Von Baer had stated ‡ that, it gradually rises from its deeper situation, towards the surface of the yolk, and that, finally bursting or being dissolved there, its contents are allowed to flow over the surface of the yolk. This process he also described in several other animals as proceeding in a similar manner; and he supposed that the germinal substance from the vesicle was thus diffused over that part of the ovum which is most closely related to the subsequent changes of development. He regarded the canal of the yolk as the remains of a passage through which the vesicle had been carried to the surface. Newport, on the other hand, is quite confident that no such passage of the vesicle to the surface occurs in the ova of Batrachia, and that the vesicle most probably dissolves or disappears in its situation below the germinal part of the yolk. From the facts he has pointed out, Newport infers that the germinal vesicle is burst or destroyed by the development of the progeny of cells within it, and that the cells thus set free are mingled with the rest of the yolk. It belongs rather to the history of the changes which the ovum undergoes after fecundation, than to our present subject, to trace the relation between the cell progeny of the germinal vesicle now described, and the cells of embryonic formation afterwards developed; but it may be proper here merely to mention that from the concurrent testimony of several observers, it seems probable that the origin of the blastodermic cells is closely connected with a combination of the vesicles or cells from the germinal vesicle with the other solid elements of the yolk-substance. To this process of cell formation the change of segmentation seems, in the Batrachia, as in all other animals, to be the necessary prelude.

It may be proper here also to state, in conclusion, that Newport has shown that the process of segmentation begins by a fissure which passes in a determinate direction through the canal of the yolk.

Although the statement of Prevost and Dumas as to the existence of an aperture in the membranes of the ovum, through which they supposed the spermatozoa might be introduced in fecundation, has not yet been confirmed by subsequent observers, but has on the contrary, met with an explicit denial from Von Baer, Newport, and Remak, after a very careful examination by these authors; and although it would appear, from Newport's statement, that the spermatozoa penetrate the vitelline membrane of the frog's egg over a considerable portion of its surface, yet the discoveries which have in the last few years been made as to the existence of the micropyle in fishes and some other animals, are of so unexpected a kind, that we must not regard this point as altogether settled. Dr. Ransom, indeed, in some observations communicated to me, has stated his belief that a micropyle may still be discovered in the membrane of the Batrachian ovum. The statement of Prevost and Dumas on this subject is so precise that it deserves to be recorded in their own words. — "On remarque ensuite qu'il existe au centre de l'hémisphère brun une tache circulaire très regulière, jaune, et marquée d'un point opaque dans son milieu. Celuici provient d'un petit trou dont les deux membranes sont percées, ce qui met à découvert la bouillie brune que renferme l'ovule. Pour s'en assurer il suffit de vider l'œuf et d'examiner à la loupe les membranes transparentes qui sont restées intactes dans toutes leurs parties, sauf l'endroit qu'on a piqué pour évacuer la pulpe qu'elles contenaient." *

The observations of Von Baer, Rusconi, Newport, and myself have shown that with certain differences in the form and structure of the external membranes, the colour of the yolk-substance, &c., previously referred to, the structure of the ovum, and the phenomena of change at the time of its discharge, are essentially the same in the Newts as in the common Frog.

A few observations which I have made on the Menobranchus lateralis and Siredon mexicanum, show that the Perennibranchiate Amphibia agree very closely with the

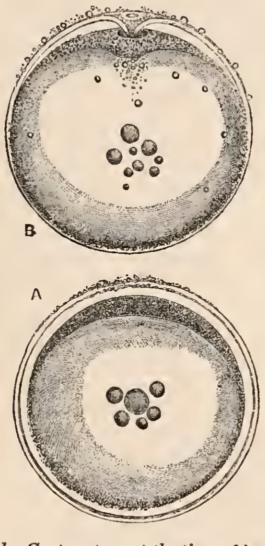
* Loc. cit. p. 176.
† Loc. cit. p. 177.
‡ Epistola de Ovi, &c., Fig. xxv.

* See Deuxième Mémoire sur la Génération:— Développement de l'œuf des Batraciens, &c., par MM. Prevost et Dumas, in Annal. des Scien. Nat. tom. ii. 1824, p. 104.

Salamandrina in regard to the structure and formation of their ova.

Osseous Fishes.—The ovarian ova of Osseous Fishes, while they bear a general resemblance to those of Vertebrata, among which they come nearest to those of Batrachia, are distinguished by several marked peculiarities. They are of middle size, and possess a strong external covering formed within the ovary. The yolk-substance contains several kinds of elements ; and the germinal vesicle is of considerable size. The external membrane is thick, strong, and elastic, and of a peculiar porous structure. The yolk-substance contains a large quantity of clear fluid, in which the albuminous granules and yolk corpuscles and the oil globules are suspended, the latter usually of large size and few in number ; the germinal layer or disc is limited to a part of the yolk, varying in size from about a sixth to a half of the circumference, and the process of segmentation in this part after fecundation is consequently more limited than in Mammalia and most Batrachia ; but more extended than in birds or scaly reptiles. The germinal vesicle contains subdivided or multiple maculæ. I now proceed to give a few details with respect to these several parts of the ovum.

Fig. 66 *.



Ovum of the Gasterosteus at the time of impregnation. (*From Ransom.*)

A. An ovum of the Stickleback eight or ten minutes after impregnation, showing the clear respiratory space formed immediately upon the access of spermatozoa between the external membrane and the surface of the yolk. Towards the upper part of the figure the situation of the micropyle is indicated by the small projections in the external membrane ; towards the same or upper part of the yolk the germinal disc or layer is easily distinguished from the clearer part of the yolk ; and in the middle a few large coloured oil globules.

B. The same ovum about three minutes after impregnation, showing somewhat in profile the funnel of the micropyle descending into a depression on the upper surface of the germinal part of the egg. In consequence of impregnation, however, the funnel of the micropyle has begun to rise out of the hollow, and the respiratory space to be formed by the separation of the external membrane from the surface of the yolk.

The yolk-mass or yolk-substance consists, in the more mature ovarian ova, of three parts : viz., the clear fluid, which is in great abundance and occupies chiefly the centre and the lower part of the ovum; the superficial layer of fine granules, with the vesicular corpuscles; and the large oily globules, which from their less specific gravity are usually situated towards the surface and on the upper side. In a number of fishes the clear fluid, which has an acid reaction, becomes immediately turbid or quite thick by the deposit of granular substance when water is added to it. This change is very apparent in the ova of the trout or salmon, which, when placed in water, retain their natural clearness and colour so long only as the coverings are entire ; but immediately on their being divided so as to allow of the action of water on the contents, the whole yolk is suddenly precipitated as a thick and somewhat tenacious granular mass. The albuminous matter which surrounds ova that have been spawned has an alkaline reaction. It is an interesting fact, that in these ova, when imbibition of water takes place as a consequence of fecundation, no precipitate follows ; but that in unfecundated ova left for some time in the same circumstances without fecundation, though unbroken, turbidity ensues ; so that by the difference of internal appearance the fertile ova soon come to be easily distinguished from those which have not been fecundated.* The solid elements of the yolk-substance appear to be in general of three kinds for some time before the ovum has arrived at maturity : viz., 1st, a quantity of small granules comparable to the granular yolk-substance of the primitive ovum ; 2nd, collections of clearer vesicles and globules interspersed with the first, and in general partly mixed with them and partly situated in a deeper layer ; and, 3rd, the large oil globules. These last are usually somewhat coloured ; they are comparatively large, and in some fishes are very few in number, and even reduced at last to only one, which is then of proportionally large size. In all fishes, the number of oil globules appears from the observations of Retzius gradually to diminish as the ova approach maturity.† The large oil globules float quite freely in the fluid of the yolk ; so that from their greater lightness they always rise towards the side of the ovum which is turned uppermost ; but the other elements of the yolk-substance, and especially the small granules of the germ-disc, come in the mature ovarian ovum to occupy one side of the yolk, and, as they form a coherent layer, do not move readily from this place. The smaller granular par-

* See a paper by Dr. Davy in the Proceed. of Roy. Soc. of Lond. 1852, p. 149.

† See Retzius in Müller's Archiv. for 1855, p. 34.

ticles become more and more circumscribed in a layer on one side of the egg as it approaches maturity, so as to form a germinal disc; and this occurs independently of fecundation.

The germinal vesicle is not easily perceived in the ovarian ovum when it has attained some size. This proceeds in part from its extreme delicacy and transparency, and also from the opacity of the granules of the yolk within which it is situated. But it is to be observed also, that it disappears proportionally sooner than in other vertebrate animals. It is of considerable size in proportion to the rest of the ovum, having a diameter not unfrequently of $\frac{1}{50}$ or $\frac{1}{60}''$ in ova of $\frac{1}{20}''$. It is never to be found in ova that have left their capsules in the ovary; and according to Lereboullet's* observations in the pike and perch, it has already disappeared for a considerable time before it attains complete maturity. In the earlier stages of the growth of the ovum the germinal vesicle contains numerous distinct maculæ; but in the progress of development these multiply to a great degree, so that the vesicle is at last completely filled with fine clear cells, or brilliant vesicles, and extremely minute granules. When the vesicle bursts, its contents are dispersed over the yolk, and very probably are mingled or combined with the layer of germinal granules; but it is not probable, as Lereboullet supposes, that the whole of the formative layer of the germ (afterwards undergoing segmentation) is produced from the effused contents of the germinal vesicle. This multiplication of the maculæ and filling of the germinal vesicle with fine cells appears to be of an analogous kind to that which has been described by Vogt and Newport in the Batrachia; and it seems not improbable that in both classes of animals the dispersed maculæ may in some way or other, not yet fully ascertained, contribute to the origin and development of the blastodermic cells in the formation of which the process of segmentation results. It appears certain at least that, after the disappearance of the germinal vesicle and the dispersion of its contents, a marked change takes place in the disposition of the germinal part of the egg by its granular disc or layer becoming more circumscribed and distinct; and, as Lereboullet supposes, it may then be mingled with the brilliant points which proceed from the contents of the germinal vesicle.

The process of segmentation, into the description of which it is not intended at present to enter, is co-extensive with the granular layer or germinal disc of the ovum. The larger yolk globules and the fat cells are not immediately concerned in this process.†

* Resumé d'un Travail sur l'Embryogénie du Brochet, de la Perche, et de l'Ecrevisse, in Annal. des Scien. Nat. 1854, tom. i. p. 237. *et seq.*

† M. Coste (Comptes rendus, 1850, vol. xxx. p. 692.) has described the germinal disc as being formed only after fecundation; but from the observations of Vogt, Aubert, Lereboullet, and Ransom, it is ascertained that it exists previously.

The membranes of the ripe ovarian ovum of osseous fishes have been described by most recent observers as two in number; viz. 1st, the external tough membrane which some have called chorion or shell-membrane, and others vitelline membrane, which possesses a peculiar structure, hereafter to be described more particularly; and, 2nd, an extremely delicate film of membrane lying close to the yolk-substance and destitute of visible structure. The latter of these membranes is just discernible in the ovarian egg at the later periods of its growth; but in ova of two thirds their full size I have failed to perceive it. Dr. Ransom has observed, that in the Stickleback, Gasterosteus aculeatus, this membrane becomes more distinctly marked off from the substance of the yolk subsequent to impregnation, and that it follows the inflections of the surface of that substance during segmentation; from which he infers, that it is not to be compared with the vitelline membrane as heretofore described by authors in the ova of other animals. The observations which have been obligingly communicated to me by Dr. Ransom leave no doubt as to the existence of this inner membrane, and have shown the new and interesting fact that it is possessed of some vital contractile power. It seems probable that it proceeds from a consolidation of the outermost layer of the basement or clear substance of the yolk, in a manner somewhat analogous to the zona pellucida. But I refrain from saying more of it at present, as Dr. Ransom will ere long probably communicate his observations to the public in detail.

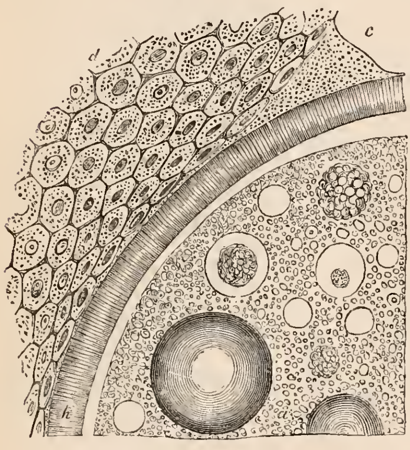
The external membrane of the Fish's egg which has been deposited in spawning or has been extracted from the ovary when approaching maturity, presents a remarkably well defined line internally, and is also generally smooth on its outer surface. In some fishes, however, as the perch, it is covered externally with villous, reticular, or other appendages, which serve to connect the ova in masses or strings, in the same manner as occurs with the albuminous matter added to the ova of some Batrachia, but in a less degree. In other instances, as the Stickleback, these villi or projecting processes are limited to one portion of the exterior. This membrane possesses considerable thickness and tenacity, and usually gives the ovum a nearly regular spherical form when imbibition is complete, as is the case after impregnation. Previous to that change, however, the outer covering of the Fish's egg is more yielding, and possesses so little elasticity, that it usually retains dimples or impressions made upon it from without. Two peculiarities of structure have been observed in this membrane which both merit farther attention, and one of which is of great interest.

The first of these to which I will refer is the dotted or porous structure of the external membrane. Von Baer* had remarked that the external membrane of the ova of the Cyprinus

* Entwickelungsgesch. der Fische, Leipzig, 1835.

genus was not entirely homogeneous, but was marked through its thickness with fine lines set perpendicularly to the surface. Vogt observed a similar structure, and described it more fully in the Salmonidæ.* More recently attention has been particularly called to it by the fuller description of the structure of the egg coverings in the Perca fluviatilis by Professor Müller of Berlin. In this fish Müller described the radiated lines as produced by fine tubes which pierce the whole thickness of the external membrane, beginning with cup or funnel-shaped dilatations on the exterior, preserving a nearly equal diameter throughout, and terminating on the inner surface.† The tubes have a slight spiral winding as they pass through. That they are really hollow tubes Müller ascertained by finding that he was able to press portions of the coloured oily contents of the yolk through them. Müller farther observed, that in the perch each tube is set in a small prism, which terminates by a hexagonal end on the outer surface. According to Dr.

Fig. 67 *.



Part of the ovarian ovum of the Salmon.

Semi-diagrammatic view of the section of a portion of the yolk, porous membrane and external layer of cells in an ovarian ovum of the salmon of $\frac{1}{40}''$ in diameter. *a*, portion of the yolk substance showing the various granules, granular and nucleated corpuscles, and oil globules composing it; *h*, section of the porous or dotted external membrane; *c*, portion of the outer surface of the same turned towards the observer so as to show the punctated or dotted marking produced by the external apertures of the fine canals which run through the membrane; *d*, the flat surfaces of the nucleated cells (epithelial or granular) which line the ovicapsule, between which and *h* they are seen edgeways lying close along the outer surface of the dotted membrane; a granular or dotted appearance in the contents of these cells seems to indicate their conversion into the dotted membrane, which is probably formed in successive layers from the exterior. The diameter of these cells is $\frac{1}{1250}''$, that of their nuclei $\frac{1}{3300}''$.

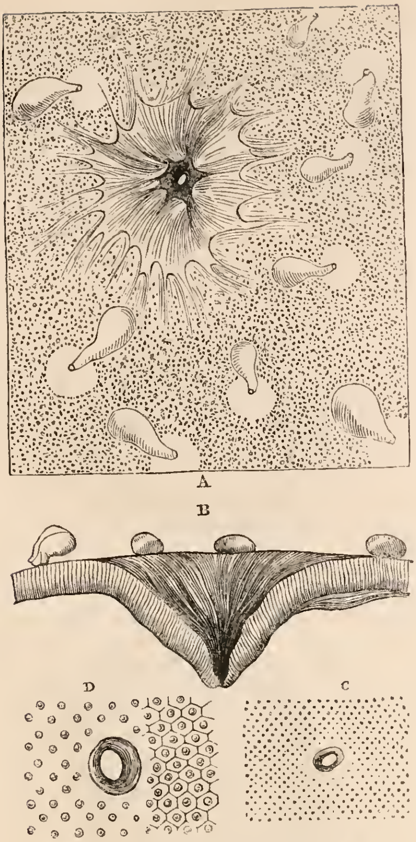
* Embryogénie des Saumons, Neufchatel, 1842.
† Müller's Archiv. for 1854, p. 186.

Ransom's observations, however, it appears that the structure described by Müller in the perch is peculiar to that fish, and belongs only to an outer covering superadded to the surface of the dotted membrane, which last resembles in all respects that of other fishes. This outer covering appears to be of cellular origin; and Dr. Ransom thinks it may be due to the separation of the tunica granulosa along with the ovum. The diameter of these tubes in the perch is about $\frac{1}{10000}''$. In most other fishes the fine lines which appear to be tubular are much smaller. I have observed them in several fishes, and have rarely found more than ten of these tubes in the breadth of $\frac{1}{1000}''$, and the tubes themselves or double lines bounding them were not more than $\frac{1}{25000}''$ or $\frac{1}{30000}''$ in breadth. In looking at the flat surface of the membrane the ends of these tubes give the appearance of a finely dotted structure to the membrane. It is quite possible, however, even where they are finest, to perceive the circle or lumen of the tube by using a high magnifying power; and I have thought that I could also in the salmon perceive a hexagonal marking of the intervals between the pores (see *fig.* 68 * D); but in this fish the size of the pores is only a third of that of the tubes in the perch as described by Müller, and the structure must be of a different kind according to Ransom's observation. All recent observers have recognised this structure in the external membrane of the fish's ovum. Müller conceived that the tubes he had observed in the perch might be connected with the introduction of the spermatozoa into the ovum; but Dr. Ransom does not find these tubes to pass entirely through the outer membrane of the perch's ovum, and has observed that the part of the true vitelline or dotted membrane which admits the spermatozoa is destitute of the additional layer; and it will immediately be shown that in all fishes a special and more direct passage for the admission of these bodies through the dense membrane is provided, constituting the second peculiarity of structure in the covering of the Fish's ovum before referred to.

The interesting discovery of an aperture in the external membrane of the ovum of osseous fishes is due to Dr. Ransom of Nottingham, who observed it first in two species of Stickleback or Gasterosteus, and afterwards in other fishes. This author made the farther interesting observation in the first-mentioned fish, that in impregnation the spermatozoa entered the ovum only through this aperture or micropyle. As this is the first instance in which the existence of this aperture and its relation to the process of fecundation have been ascertained by direct observation in a vertebrate animal, I will describe it more fully from Dr. Ransom's paper to the Royal Society of London*, and from farther information which he has obligingly furnished to me in private. I may also mention that I have fully confirmed Ransom's observations as to

* Proceedings of Roy. Soc. 1854, Nov. 23rd.

Fig. 68*.



Micropyle of the ovum in Osseous Fishes.

A. Enlarged view of a quadrangular portion of the surface of the mature ovarian egg of the Stickleback containing the micropyle from above. In the outer part of this figure the general dotted appearance of the membrane is seen, and here and there the pediculated flask-like processes attached to the membrane in this fish in the vicinity of the micropyle; the radiated shading represents the appearance of the funnel-shaped depression leading to the aperture of the micropyle, which is seen in the centre of the space it encloses.

B. Transverse section of the dotted membrane and funnel of the micropyle of the same egg somewhat more enlarged, seen in profile; the aperture of the micropyle is seen towards the point of the funnel. This view is semidiagrammatic, and the fine canals passing through the membrane are represented fewer and wider than they are in nature.

The diameter of the whole ovum was about $\frac{1}{20}''$; the thickness of the external membrane $\frac{1}{1000}''$; the width of the base of the funnel about $\frac{1}{150}''$; the depth of the funnel $\frac{1}{200}''$; the diameter of the micropyle aperture at the apex $\frac{1}{3300}''$.

C. Small portion of the membrane at the apex of the funnel containing the aperture of the micropyle pressed flat, magnified 500 diameters; from the trout's egg.

D. A similar portion of the membrane magnified 1000 diameters. The lumen of the canals is seen, and an indication of hexagonal division of the spaces between them, represented somewhat too distinctly in the figure.

the existence of the micropyle in the ova of several fishes; and though I have not yet been so fortunate as to perceive the spermatozoa actually passing into the ovum through this aperture, the accuracy of Ransom's observations on this as well as on other points leave little doubt as to the fact stated by him.

The micropyle in the Gasterosteus, as described by Ransom and observed by myself, is a considerable funnel-shaped depression in the outer membrane, which projects inwards on the granular substance of the yolk, so as to indent this layer to some depth, and probably to reach near to the germinal vesicle, which lies imbedded within the germinal layer. The inner narrow end of the funnel terminates in a distinct rounded or elliptical mark, with a fine but distinct line bounding it, which has all the appearance of a foramen, and which is either an open passage or one which is closed only by an extremely delicate structure. The funnel-shaped depression leading to the micropyle may be easily seen on the surface of the egg of the salmon or trout when slightly dried of the adhering moisture, and is of such a size that it may be perceived with the naked eye or with a lens of low magnifying power. In order to perceive the micropyle itself, however, or pore in the point of the funnel, it is necessary to remove from the egg that portion of the dotted shell membrane containing the funnel; and having freed it from the adherent granules of the yolk-substance by careful washing, for which Ransom has recommended a solution of acetate of potash, this part of it may be viewed under pressure with great ease with a magnifying power of 200 or 300 diameters. The porous structure of the membrane is then seen to continue very nearly up to the margin of the micropyle. This last has a diameter of from $\frac{1}{3000}''$ to $\frac{1}{6000}''$. The appearance of a double outline surrounding the micropyle proceeds from the circumstance that, in looking through the funnel we see at once two portions of the narrowing wall of the passage of different widths.

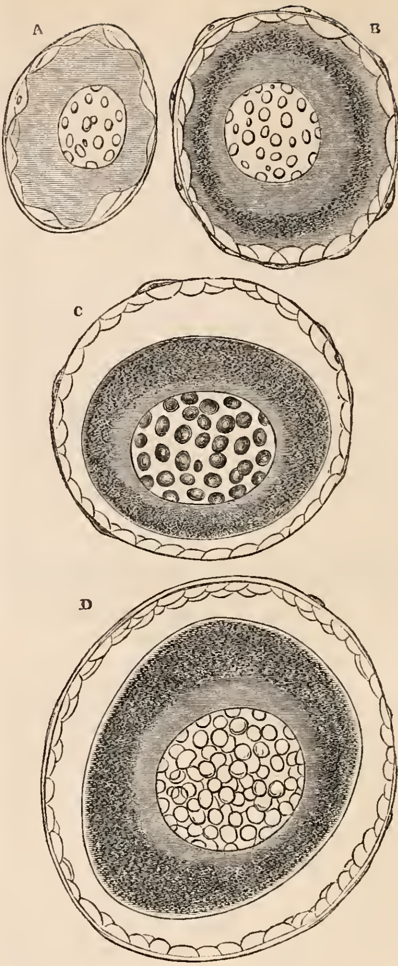
In Ransom's experiments, very soon after spermatic fluid was placed in the water round the ovum of the Stickleback, several of the spermatozoa were perceived to pass in at the micropyle; and immediately upon this water was imbibed, and the space named the respiratory chamber was formed between the yolk surface and the external membrane; a change which in this fish did not take place in the unfecundated ova, but which in some others occurs without impregnation. It is from this fact apparently that Ransom is inclined to the opinion that the micropyle may be closed by a very delicate membrane, which in fecundation is removed or broken through by the entrance of the spermatozoa; but with regard to this point there is still some uncertainty. The germinal vesicle previous to its disappearance is imbedded below the superficial layer of yolk-substance in a stratum of granular matter; and Ransom conceives that at the time of the rupture of the vesicle, this granular matter being mingled with the contents of the vesicle, the more immediately germinal part of the egg is formed from the mixture of the two. However this may be, it seems not improbable, from the observations now referred to, that the spermatozoa are conveyed directly to the germinal part of the egg by the funnel of the micropyle. I shall afterwards have to state the more numerous instances in which, following its first discovery by J. Müller in the Holothuria, a micropyle has been detected in the ova of Invertebrate animals; and I may attempt to show the great importance of this aperture in connection with fecundation in ova with thick external coverings to which the spermatic substance does not gain access till the later periods of their formation. The accompanying figures of the micropyle in the Stickleback will give a sufficiently clear view of this remarkable structure. At present it may be permitted to remark that, if we consider the size of this aperture, and the ease with which it may be found in the ova of fishes by an observer whose attention has been called to its existence, together with the fact of its having been so long overlooked previously, there is much ground for caution as to negative statements as to the existence of a similar aperture in the ova of other animals. I have already made allusion to this subject in the previous sections, in which I have stated that Dr. Ransom has expressed to me his firm conviction, founded on observations, that the micropyle exists also in the ova of Batrachia. At the same time it is quite probable that such an aperture may only exist or be required for the admission of the spermatozoa when fecundation is of late occurrence, and when the covering membrane of the ovum is so dense as to resist the penetration of the spermatozoa through its solid substance.

It is right also to mention that the existence of this aperture, or rather the funnel leading to it, did not entirely escape the observation of preceding physiologists. The accurate Von Baer, in his work on the development of Fishes*, has described in the Bream (Cyprinus blicca) a funnel-shaped depression of the external membrane, which reached nearly to the surface of the germ; and he observed that this funnel was effaced as soon as the imbibition of water took place. He considered this aperture as most probably owing to the escape of the germinal vesicle from the surface of the yolk and through the coverings of the ovum, in the same manner as he had described in the frog†, and did not therefore conceive it to serve any immediate purpose in connection with the introduction of the spermatozoa. Dr. Ransom has observed that the effacement of the funnel which he had seen in the Stickleback is not invariably the consequence of fecundation in the Fish's ovum; for in the salmon and trout

* Entwickelungsgeschichte der Fische, Leipzig, 1835, p. 9. figs. 1. and 2.

† De Ovi Mammal. &c., pl. xxv.

Fig. 69.*



Development of the ova of Gasterosteus.

A. B. C. D. Four ova of the Stickleback in the earlier stages of their development within their ovisacs.

In that figured at A, which is the earliest, $\frac{1}{400}''$ in diam., the germinal vesicle placed near the centre has scarcely any perceptible membrane or wall, but resembles a gelatinous mass in which the small number of maculæ are developed: there is as yet no yolk, but only a slightly turbid fluid substance filling the space between the ovisac and the germinal vesicle: delicate epithelial cells project from the inner surface of the ovisac.

In B. $\frac{1}{250}''$ the maculæ have increased in number, the germinal vesicle, as well as all the other parts, has increased in size, the fine granules of the yolk substance have begun to be deposited towards the periphery, but there is as yet no vitelline membrane. The wall of the ovisac is now more distinct, and besides the internal cells, there are seen on the exterior the nuclei of external flattened cells.

In C. $\frac{1}{180}''$ the maculæ have become more numerous and distinct; the yolk granules are more opaque and in greater quantity, and the mass of the yolk more circumscribed, a clear space now intervening between it and the wall of the ovisac.

In D. $\frac{1}{140}''$, although the number of maculæ has greatly increased by endogenous multiplication, the germinal vesicle has not now undergone an enlargement proportional to that of other parts of the egg and ovisac: the granules of the yolk, especially towards the surface, are much increased, and a narrow clear marginal space on the surface now indicates the commencement of the formation of a zona or vitelline membrane. This appearance is also slightly perceptible in *fig.* C.

The dimensions of the several parts in these different specimens were as follows:

	A.	B.	C.	D.
Ovisac - -	·0025	·004	·0056	·007
Yolk - -	—	—	·0042	·005
Germinal vesicle -	·001	·0016	·0025	·0026
Maculæ - -	·00015	·00018	·00025	·0003

he found the funnel-shaped aperture to remain for some time after the completion of fecundation, and in none of the fishes he has observed does he conceive the aperture of the micropyle to be closed.

The ova of osseous fishes appear to take their origin within the rudimentary follicles or ovisacs of the ovary much in the same manner as those of the Batrachia. The earliest part of the ovum that can be distinctly seen within the follicle is a vesicle of about half the diameter of the primitive follicle itself. A little later this vesicle is seen to be surrounded with a clear, jelly-like substance, in which some small dark granules are deposited chiefly towards the surface of the vesicle. There is as yet no enclosing membrane, but the follicle is seen to be lined by a layer of extremely delicate hyaline cells, often difficultly perceptible. The earliest recognisable part of the ovum, therefore, is the germinal vesicle; which, as in other animals, has soon deposited round it the clear gelatinous basement-substance of the yolk, in which the opaque yolk granules soon make their appearance. There is not at first any vitelline or other membrane enclosing the primitive parts of the egg, and indeed it is a considerable time before any such membranes are formed. The deposit of vitelline granules increases rapidly, so as to give the yolk considerable opacity; afterwards larger globules appear, and seem to increase by endogenous multiplication.* The oil globules are at first small, and equally diffused through the whole yolk; it is only in the later stages of formation that they unite into fewer and larger globules.† The granular or primitive yolk-substance continues to surround more immediately the germinal vesicle till the period when this vesicle is ruptured, and is probably spread over the germinal disc of the egg. Similar granules also occupy, however, in a layer the surface of this part of the egg previous to the rupture of the germinal vesicle; so that it is not probable that the germinal disc owes its origin, as Coste states ‡, entirely to the effusion of the contents of the germinal vesicle.

* Lereboullet, loc. cit.

† Retzius, loc. cit.

‡ Hist. gén. et part. du Développ. des Corps orgau. tom. i.

The ovum receives its firm porous membrane while within the ovarian capsule, but only in the latter part of the time of its formation. This membrane lies very close to the inside of the ovisac, is at first comparatively thin and destitute of apparent structure, and gradually increases in thickness towards the time of its approach to maturity. At the same time a remarkably thin pellicle may be distinguished close to the surface of the granular yolk-substance, scarcely meriting the name of membrane. As already remarked, it is difficult to determine what is the true homological signification of these membranes. The inner one might by some be regarded as a representative of the zona pellucida, or a consolidated pellicle on the surface of the yolk, though it must be admitted that Ransom's observation, that it follows the segmentation, is opposed to this view, and makes it more probable that it is only a part of the yolk itself. The origin of the external porous membrane I am inclined to connect rather with the interior of the ovarian follicle; but whether by exudation from it, or by amalgamation of the innermost layer of epithelial cells of the follicle, I have not yet been able to determine. I am inclined to regard the latter as most probable, and that this is the true vitelline membrane.

The manner in which the micropyle takes its origin has not yet been ascertained. It will afterwards be shown, that in a considerable proportion of those invertebrate animals in which this aperture in the egg coverings is found, it has existed from a very early period, and proceeds from the remains of the pedicle by which the ovum is originally connected with the ovarian substance. Such a pediculated connection has certainly not yet been observed by most of those who have investigated the ovarian ovum of fishes.* Rathke, indeed, observed the appearance of the remains of a pedicle in the detached ova of the Blennius viviparus †; according to Ransom the micropyle in the Pike is not a depression, but projects from the surface like a trumpet-shaped process; and in the earliest stage of development of the ovarian ovum of Trigla hirundo, according to Leydig ‡, the shape is somewhat pyriform or pediculated, in the same manner as in some of the invertebrate animals.

On the other hand, Ransom expressly states that he has never been able to observe the slightest connection in Gasterosteus between the pedicle of the ovum by which it is attached to the ovary, and the micropyle. This aperture he says is always situated at that side of the ovum towards which the germinal vesicle and the germinal disc are placed; but these parts have no regular connection with the pedicle. The pe-

* The pedicle here spoken of is not that of the ovarian capsule containing the ovum, but of the ovum itself within the capsule.

† Abhandlung. zur Entwick. part. ii. p. 4.

‡ Müller's Archiv. for 1854, p. 376. fig. 6.

dicle, he affirms consists only of the ovarian structure, and of no part of the membranes of the ovum. From his observations on Gasterosteus, in which the projecting bodies from the porous or outer membrane in the vicinity of the micropyle enable this part to be easily recognised, he feels confident that if any pediculated connection had existed it could hardly have escaped notice.

When the ovarian ovum has attained maturity it falls into the cavity of the ovary, or that which may be regarded as ovary and oviduct united, by the rupture of the ovarian capsule in which it is contained. The walls of the ovi-capsules have by this time become extremely thin; but according to Von Baer a small stigma or non-vascular mark may be distinguished where the rupture takes place. After the ova have fallen into the common cavity they are surrounded by a considerable amount of secreted albuminous matter, by which in some fishes the ova are covered when excluded. In some this albuminous secretion serves to unite the spawn in chains or networks. In other fishes the ova are covered externally with villous projections; but the manner in which these are formed has not yet, so far as I am aware, been observed.

One of the most remarkable, but as yet quite unexplained, varieties in the external coverings of the ovum in one of the osseous fishes, is that discovered and recently described by Ernst Hackel, as occurring in the family of Scomberesoces.* This consists in the formation, in the space between the surface of the yolk and the vitelline membrane (that is, the porous membrane), of a layer of long and very distinct fibres, which are wound somewhat spirally, but irregularly, over the surface of the yolk. Hackel has traced the gradual formation of these in fresh specimens of Belone from points on the surface of the yolk-substance; and in other genera he has observed several varieties in the forms of the fibres. They are on an average about $\frac{1}{3500}''$ thick, and long enough to surround the egg several times; and they appear to resemble the fibres of the elastic yellow tissue more than any other animal substance, but do not entirely agree with them. In the meantime we must suspend our judgment as to this very extraordinary addition to the surface of the ovum until farther observations shall have been made as to their distribution in various fishes or other animals, and as to their relation to the development of the embryo. †

Invertebrate Animals.—The ova of Invertebrata may be considered under two principal divisions, according as they present more of the large-celled or of the finely granular yolk-substance. The ova of the first kind are usually of a larger size; they possess a larger germinal vesicle, and often a divided or multiple macula; and the process of segmentation in them is either partial, that is, limited to one part of the surface of the yolk, or it occurs in a different manner on the upper and lower sides of the ovum. In these there is, in fact, nutritive as well as formative yolk. In the other division of animals the yolk is finally molecular, or is mainly composed of smaller granules, and is chiefly of the formative kind; segmentation usually involves the whole yolk, or if not so, is very nearly complete: the germinal vesicle is generally clear, and the macula most frequently single, and well marked. It is true that the form and structure of the ova of Invertebrata presents many and considerable varieties, as might indeed be expected among animals of such diversity of organisation as belongs to the great divisions of the Radiata, Articulata, and Mollusca; but still it is to be observed that as a greater degree of simplicity exists in the form and structure of the primordial elements than in the more developed textures and organs of animals, so also we find that much closer analogies may be traced among these elements in the lowest classes of the animal kingdom. We meet, therefore, with little difficulty, even in the most diverse tribes of the Invertebrate animals in tracing the correspondence of the essential parts of the ovum; and we are enabled also to trace a more close analogy between these and the corresponding parts in the Vertebrata than might have been expected. We are therefore warranted in applying to them similar designations; and we have daily increasing reason to trust to observations made on the ovology of the lower animals as the means of extending the knowledge of the reproductive functions in Vertebrata and in Man. Thus the recent discovery of the micropyle aperture in some animals, and the certain and clear observation of the penetration of the sperma-

* Müller's Archiv. 1855, p. 23. See plates IV. and V.

† Some time after the above was in the hands of the printer, I received the first and second parts of the seventh volume of the Zeitsch. für Wissen. Zool., containing a notice of the discovery of the micropyle in the Salmo salar, and S. fario, by Professor Bruch of Basle. The observations leading to this discovery were made in the winter of 1854-5; and it is right to state here, that Dr. Ransom's discovery of the micropyle in the gasterosteus, which was communicated to the Royal Society on the 23rd of November, 1854, was made in the months of June and July previous; and these observations had been communicated to Professor Sharpey and myself in August and September. In the beginning of January, 1855, Dr. Ransom informed me by letter of his having found the micropyle also in the Trout, and a few days later in the Salmon. I then saw the micropyle in the ova of both of these fishes; and I have since examined it minutely in the Stickleback, and have confirmed in every particular Dr. Ransom's statements. The existence of the micropyle in these Vertebrate animals has thus been established by several independent observations; and I believe that no one who uses the proper means can fail to detect it in these and other fishes. Professor Bruch's observations were chiefly made on the ova after impregnation, which may explain the reason of his having failed to perceive the connection pointed out between this aperture and the depression in the centre of the germ disc. Bruch was like myself unsuccessful in perceiving the entrance of spermatozoa by the micropyle. His measurement of the micropyle in the Salmon and Trout does not agree with mine, making it much smaller.

tozoa into the ovum in others, suggest novel and more general and extended views of the process of fecundation, and while they add certainty to the more limited observations of the same kind made upon animals higher in the scale, tend to prevent the adoption of partial views in regard to these functions of the animal economy.

It is principally among the more highly organised Invertebrata that we meet with that form of ovum in which the nutritive is combined in considerable quantity with the formative yolk, and in which segmentation is partial, such as the Cephalopoda, Insecta, Arachnida, Myriapoda, Crustacea, and some of the Articulate Worms. In by far the greater number of the Mollusca, such as Gasteropoda and Acephala, the ova belong to the smaller kind with more or less complete segmentation, as also in most of the Annelida, as Hirudinea and Lumbricina, the Nematoid, Cestoid and Trematode worms, with the Planariæ, the Rotifera, Echinodermata, Bryozoa, Acalephæ and Polypina.

I now proceed to give a short statement of the principal facts that have been ascertained as to the structure of the ovum in these animals, and to state some details with regard to some of those which are either best known or which present phenomena of the greatest interest.

1st. *Large-yolked Ova with partial Cleavage. Cephalopoda.*—The ova of this class of animals have already been referred to in connection with those of birds, scaly reptiles, and cartilaginous fishes, to which they present in some respects a greater analogy than to those of almost any of the Invertebrata. The considerable size of the germinal vesicle with its multiple maculæ, the large mass of the coloured yolk (nutritive), composed of conglomerated masses of yolk corpuscles, and the very limited extent of the process of segmentation, which affects only a round disc of the germinal part of the egg, are all characters in which the ova of the Cephalopoda, at least the Sepia and Loligo, which have been fully examined, are ascertained to be similar to those of the large-yolked group. We owe the most of our knowledge of the ova of this class and their development to Kölliker's interesting treatise, published in 1844.* The ova of the Sepia are deposited singly, but are attached in numbers close together by pedicles to the stalks of Algæ and other marine productions. Those of Loligo are arranged in small masses, in which a number are enclosed in a general bag or covering of gelatinous matter, which is attached along with others of the same kind by means of pedicles. I have found those of Sepiola also thus enclosed in small pyriform capsules.

The ovum of Cephalopoda possesses a firm laminated external covering or chorion, which in some is darkened on the surface by the colouring matter or ink, in others is transparent and colourless. Immediately within this outer membrane is situated a structureless vitelline membrane, containing the mass of yolk-substance, which is separated from the membrane by a slight interval. It appears to be ascertained that the chorion is formed by superposition on the surface of the ovum during its descent through the oviduct.

In the ovary the ova are contained in slender capsules, attached to the rest of the ovary by narrow pedicles. When ripe the ova escape from the capsules, in some species by an irregular laceration, in others by a more regular and defined opening, and, falling into the cavity of the ovary, pass thence into the oviduct, through which they are finally excluded. Fecundation is believed to occur soon after the escape of the ova from their ovicapsules or in the earlier part of their descent through the oviduct; but this process has not, so far as I am aware, been directly observed.

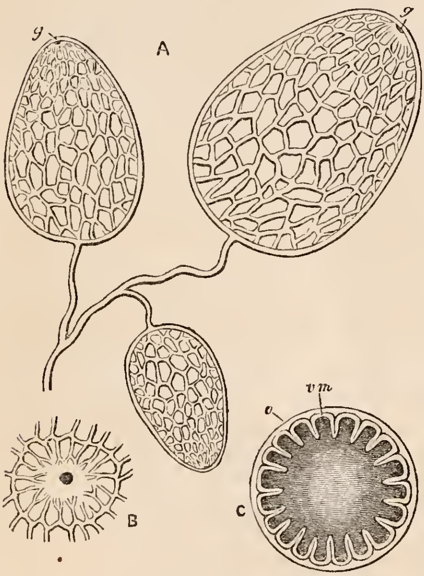
The ova of the common Sepia officinalis have an oval form, one end being much narrower than the other. It is at this the pointed extremity or narrow pole of the egg that the germinal vesicle is situated, while the egg is in the ovary, close under the vitelline membrane; and it is at this part also that, at a subsequent period, the process of segmentation and the first formation of the embryo take place. The narrow end is therefore the germinal pole. This extremity of the egg is always turned to the opposite side from the pedicle of the capsule, which is attached to the middle of the blunt or wider end.

One of the most remarkable peculiarities in these ova, is the extraordinary change which the outer part of the yolk and the vitelline membrane undergo during the greater part of the time occupied by the growth of the ovum in the ovary. This change, of which the appearance had been known to some previous observers, was first accurately described and explained by Kölliker. From his observations it appears that at first the ovarian ova are quite smooth on the surface, and that at the time of complete maturity of the ovum, or after its escape from the ovary, the vitelline membrane and surface of the yolk are also quite smooth; but that in the intervening time, that is, during the greater part of the period of its growth, the surface of the yolk is indented or marked with peculiar grooves, into which folds of the vitelline membrane pass so as to line them to the bottom, somewhat after the manner in which the pia mater descends into the sulci of the brain, but without the same convoluted form. This has been represented by Kölliker in the Sepia, and I have observed it in this genus, and have confirmed in every particular that author's statements as to this change. It appears that at first these inflections of the yolk and membrane begin as longitudinal folds, extending between the wide and narrow poles of the ovum, and, gradually increasing, become at last so deep as almost to meet each other in the interior of the yolk. Subsequently they are traversed by more numerous depressions.

* Entwickelungs-gesch. der Cephalopoden, 4to. Zurich, 1844.

which subdivide them; and as these cross folds are formed the longitudinal ones beome gradually shallower. The surface of the egg then presents the reticulated appearance which is shown in *fig.* 70.* On making a section through such an egg, hardened in alcohol or any other suitable reagent, it is easy to perceive that the ovicapsule takes no part in the inflections, but that they consist entirely in the grooving of the yolk, and the corresponding bending into the grooves of the vitelline membrane. This state is maintained till the ovum is approaching maturity, when the depth of the grooves or folds speedily diminishes; and these come at last to be completely effaced in those ova which have left the ovicapsule. In Loligo, it is stated by Kölliker, there are only the longitudinal folds. No satisfactory opinion has been offered as to the cause of this peculiar structure.

Fig. 70*.



Ova of the Sepia. (*From Kölliker.*)

A. Three ovarian ova of the Sepia in somewhat different stages of advancement attached by their pedicles to the ovary, and represented several times magnified. They all show the reticulated markings on the surface produced by the folding in of the vitelline membrane; *g*, the place of the germinal vesicle and possibly also of a micropyle at the small pole of the egg, in which segmentation afterwards occurs.

B. Direct view of this germinal pole of one of the ova, showing the absence of the folds towards the centre in which the germinal vesicle is situated.

C. Cross section of one of the ova, showing at *o* the unfolded or smooth ovarian capsule, and at *v m* the folded vitelline membrane.

Towards the narrow pole of the ovum, the folds now described become less marked; and they are entirely absent just at the pole itself, so that the germinal vesicle may be seen in the smooth space which is left between them. At this place I had some expectation to find an aperture of the nature of a micropyle; and I accordingly sought for it in some specimens of the ovarian ova of Sepia which I had preserved in alcohol, but without success, perhaps on account of the opacity produced in the membranes by the alcohol, and the adhesion of the yolk substance to them. Professor Kölliker has since informed me that he believes the micropyle to exist in these ova, which I think extremely probable.

The germinal vesicle, according to this observer, remains entire and visible till the ova are mature, as may be seen by the examination of specimens hardened in alcohol. It disappears just about the time of the ova leaving the ovarian capsule; but in several instances he found it still remaining in ova that were already free. It was always gone in those ova which had regained the smoothness of their exterior.

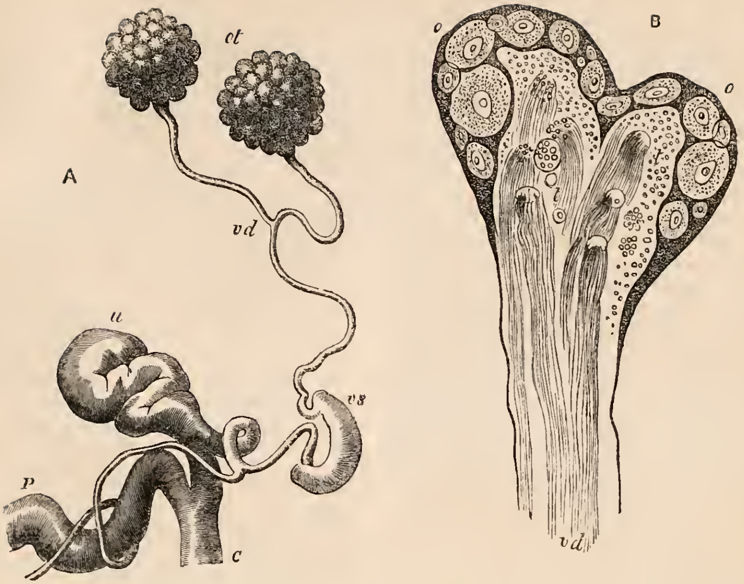
The yolk-substance of the mature ova consists entirely, excepting immediately at the seat of the germinal disc, of corpuscles somewhat similar to the vitelline tablets of the Frog's egg. At an earlier period there are heaps of fine granules of the same size, from which the corpuscles are therefore probably formed. In the earliest stage the vitelline substance is entirely composed of fine molecules — the primitive yolk — which appear to be formed in the same manner as in other animals.

The Cephalopoda furnish a remarkable example among the Invertebrata of a very limited or partial segmentation. This process, upon the detailed description of which I will not enter here, usually commences in a spot either in or more frequently near to the germinal pole, by the formation of the primitive groove which extends across the disc. The formation of the second groove, which crosses the first, the production of other radiating grooves, the separation of annular sets of segments from the periphery, and the successive steps of the process which follow, are probably determined by the same circumstances which have been referred to as related to this phenomenon in the cicatricula of the Bird's egg.

Gasteropoda.—In the greater number, if not almost all, of the remaining Mollusca, the ova differ greatly from those of the Cephalopoda, and approach more nearly to those I have classed under the groups possessing the small or middle sized yolk, which is principally or entirely formative, and which undergoes a more or less complete segmentation.* In the Pteropoda and in those of gasteropodous Mollusca, which have the male and female organs in the same individual, there is a remarkable combination of the ovary and testis in a single hermaphrodite organ, usually

* The genus Sagitta, among the Pteropoda, is, however, probably an exception to this statement, as in it, according to Darwin, the embryonal part of the yolk is distinct from the rest, or rather covers it like a ring.

Fig. 71 *.



Genital Organs of Phyllirhoe bucephalum, one of the Hermaphrodite Gasteropoda. (From H. Müller and Gegenbaur.)

A. The compound or hermaphrodite organs dissected out and represented several times magnified; *o t*, the two productive organs each composed of ovigerous and seminiferous parts; *v d*, the common excretory ducts for both kinds of organ; *v s*, the seminal vesicle; *u*, the uterus; *p*, a part of the penis; *c*, the common external vent.

B. One of the lobes of the common productive organ laid open and more highly magnified. Towards the surface *o o*, the ova are seen in different stages of development in the ovarian stroma; in the interior *t t*, the substance of the testis with spermatic cells and spermatozoa in various degrees of advancement; some of the filaments being very long; *v d*, the common excretory duct for ova and spermatozoa.

enclosed in the liver, the nature of which was for a long time involved in obscurity, and occasioned much doubt and difficulty to naturalists. The explanation of this peculiar structure we owe first to H. Meckel*, and Leuckart†; and more recently H. Meckel and Gegenbaur have described this organ particularly in one of the heteropodous Mollusca, viz. Phyllirrhoe bucephalum.‡ The outer part of this curious organ constitutes the ovary, the inner the testis; and the products of these respective organs, in leaving the seat of their first formation, pass together into an inner common cavity, and thence downwards in the excretory duct. There is, therefore, a common outlet for both. The ova and spermatozoa most frequently pass out at different times; but occasionally both these reproductive elements are seen together in the passages. It seems probable therefore that they in general meet for impregnation only in the lower part of the passages; but this apparently is not yet fully determined, and the modes of union may be

* Müller's Archiv. for 1844, p. 483., see plates xiv. and xv.

† Zur Morphologie und Anatomie der Geschlechts Organ. 1847, p. 128.

‡ Zeitsch. für Wissen. Zool. vol. v. p. 355. pl. xix.

various in different genera or families. At all events, the primitive ova and spermatozoa seem to come into contact with each other previous to the addition of the enveloping membrane.*

The ova of the Mollusca are in general of small size. The yolk consists of a viscid albuminous substance, containing suspended in it minute granules, and a variable quantity of coloured oil globules. The germinal vesicle is proportionally of considerable size; and the macula is distinct and granular. Leuckart† states that he and Nordmann have ascertained that in Lymneus, the first part of the ovum which is formed is the germinal vesicle, that the yolk-substance begins as a clear transparent albuminous matter surrounding the germinal vesicle, and, as we have seen in various other animals, the granular yolk matter is gradually deposited in this clearer part of the vitelline substance, occupying at first princi-

* The hermaphrodite gland exists in the Pteropoda, Apneusta, Nudibranchia, Infero-branchia, Tectibranchia, and Pulmonata. The Mollusca which have separate sexual organs belong chiefly to the orders Cyclobranchia, Scutibranchia, Tubulibranchia, and Cirribranchia, some Heteropoda, Pectinibranchia, and operculate Pulmonata or Cyclostoma.

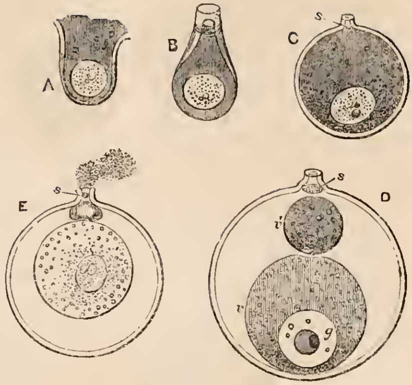
† Article Zeugung, p. 800.

pally its outer part. The vitelline membrane does not exist at first, but seems to be formed at a later period by the consolidation of an external layer of the primitive yolk substance.

The time of the disappearance of the germinal vesicle has not been determined in many of these Mollusca. Previous to segmentation a phenomenon occurs, which has now been observed in a large number of animals, but which first attracted special attention in the gasteropodous Mollusca; viz., the separation of one or more clear hyaline liquid globules of considerable size from the surface of the yolk substance, into the space between it and the vitelline membrane. This was first observed by Dumortier*, and described by Pouchet†, by Van Beneden in the Aplysia ‡, by Nordmann in Tergipes Edwardsii §, by C. Vogt in Actæon ||, and by various others. A precisely similar phenomenon has also been observed in some of the Vertebrata, as in Mammalia by Wharton Jones, Barry, and Bischoff, and in Batrachia by Newport. But though this separation of one or more hyaline globules from the yolk-substance at the time of segmentation appears to be a very general accompaniment of that process, it must be confessed that its import, either in connection with fecundation or development, has not yet been ascertained.

Acephala. — In Acephalous Mollusca the ova are generally of small size, the yolk-substance principally finely granular, the germinal vesicle clear, with a distinct macula, which last not unfrequently presents the form of a double or elongated biscuit-shaped particle. The vitelline membrane is distinct and possesses considerable strength; and there is generally a considerable space occupied by clear fluid between it and the surface of the yolk. The most interesting feature of the ova of these Mollusca is the funnel-shaped aperture which most of them possess, leading through the vitelline or external membrane into the space occupied by the yolk. This aperture, styled micropyle by J. Müller in the Holothuria, the first instance in which it was discovered, in 1850 ¶, was observed in the ova of Unio and Anodonta by Leuckart ** and Keber. †† The latter author supposed that he had observed the penetration of a spermatozoon into the ovum through this aperture, and has described with great formality and minuteness all the phenomena which he conceived were related to that process. Although Keber was correct in asserting the existence of the micropyle in these Mollusks,

Fig. 72 *.



Ova of Unio in different stages of development.

(A. B. C. and D., *from Hossling;* E. *from Keber.*)

A. The early stage of the ovum, when the germinal vesicle alone is distinguishable lying in a bulging part of the ovarian substance.

B. The same somewhat more advanced; the ovicapsule and vitelline membrane have assumed the pediculated form, and the yolk granules surround the germinal vesicle.

C. The ovum now enlarged and spherical in form, the yolk granules increased in quantity, and the pedicle narrowed so as to form a short micropyle tube; *s*, the small body taken by Keber for a spermatozoon, existing long previous to the occurrence of fecundation.

D. The ovum, &c. at a later stage; *g*, the germinal vesicle; *v*, the yolk; *v'*, the separated portion of the yolk; *s*, as in C. now enlarged.

E. A nearly similar stage of the ovum as figured by Keber. Some of the contents of the separated portion of the yolk are escaping through the micropyle aperture; *s*, Keber's alleged spermatozoon.

it appears that the body described by him as spermatozoon cannot have been of that nature, seeing that it has been proved by other observers that the appearance on which Keber's supposition was founded existed long before fecundation, and remained long after the commencement of embryonic formation in the same condition.*

The existence of a similar aperture or micropyle in several other Acephalous Mollusca has been ascertained by the recent investigations of various authors; but the actual entrance of the spermatozoa by the aperture, has not, so far as I aware, been satisfactorily observed. There seem, however, to be sufficient grounds for believing that in the Acephala, as in other animals in which it is found, the micropyle is immediately related to the process of impregnation, by affording a ready access of the spermatozoa to the yolk through the more resistent membranes of the ovum. The accompanying figures from Keber and his critic Hessling give a sufficiently clear view of

* Embryol. des Mollusques, in Annal. des Scien. Nat. for 1837, p. 136.

† Id. lib. for 1838, vol. x. p. 63. See also Pouchet's further observations in his work, Théorie positive de l'Ovulation spontanée, pl. xvi.

‡ Annal. des Scien. Nat. 1841, p. 126.

§ Id. lib. 1846, p. 147.

|| Sur l'Embryol. des Mollusques Gastéropodes, id. lib. 1846, p. 33.

¶ Archiv. 1852, p. 19.

** Article Zeugung, p. 801, Ann. 1853.

†† De Introitu spermatozoorum in ovula, &c. Königsberg, 4to. 1853.

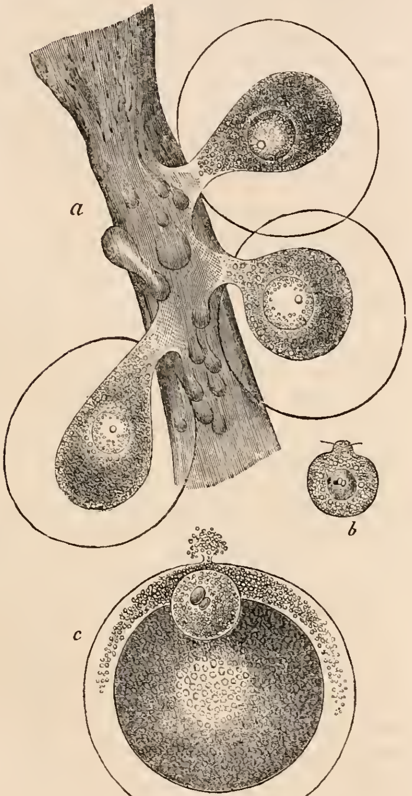
* Hessling, in Zeitsch. für Wissensch. Zool., 1854, vol. v. p. 380.; and Bischoff, Wiederlegung des von Dr. Keber bei den Naiaden, &c. Giessen, 4to. 1854.

the nature of this structure in the mature ovum of Anodonta.

In this family of Mollusca the micropyle forms a small but very apparent funnel-shaped projection from the surface of the outer membrane; and its hollow nature may easily be ascertained by the fact that the fluid and granular yolk-substance may be forced through it from within. The yolk ball is placed excentrically within the vitelline membrane, the inner surface of which it touches just at the place where the micropyle is situated.

From a variety of observations, it has been shown that the micropyle of the Acephalous Mollusca owes its origin to the early pediculated attachment of the ovum. This has been fully brought out by the observations of Hessling in Unio and Anodonta, of Leydig in Venus, and of Lecaze Duthiers in Cardium and some other genera.* From these observations it appears that the ova first arise in the ovarian stroma by the formation of the germinal vesicles, as in most other animals, each vesicle possessing a distinct single macula. These vesicles come very soon to be surrounded by some of the primitive or finely granular yolk, which gradually increases in quantity. These parts are from a very early period enclosed by a membrane which may be regarded as vitelline, but which is differently disposed from that in any of the animals previously referred to; for, instead of having a regular and complete spheroidal or vesicular form, this membrane is elongated at one part into a pedicle, so as to give the whole of the early ova a pyriform shape, and so as to attach them to the ovarian substance by the pediculated parts of the vitelline membrane. In Venus de-

Fig. 73*.



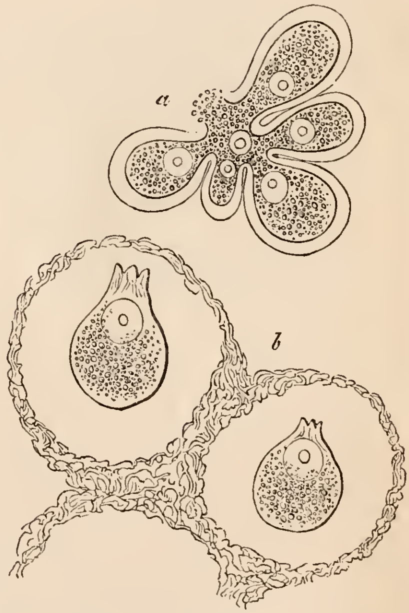
Structure and Formation of Ova in Acephala. (*From Lecaze Duthiers.*)

a. Portion of the ovary with three pediculated ovicapsules and contained ova from Cardium rusticum, magnified 400 diameters; the micropyle is afterwards formed at the place where the pedicles are detached from the secreting cœca of the ovary.

b. Unripe ovum of Spondylus gæderopus magnified 170 diameters, showing the remains of the capsule at the upper part, and the projection of the vitelline membrane at the same place where the micropyle is situated.

c. Ripe ovum of the same burst by pressure, showing the escape of some yolk granules through the micropyle and into the space between the yolk and the outer membrane. In this and the previous figure the double state of the macula is represented.

Fig. 74*.



Ovarian ova of Venus decussata. (*From Leydig.*)

a. A group of five ova in their earliest stage projecting from the ovary in their pediculated capsules: the germinal vesicles with single macula, the vitelline granules, vitelline membrane, and ovicapsule are all distinct.

b. Two ovicapsules within which at a more advanced stage the ova have become detached from their pedicles, the remains of which at the upper ends of the ova form the micropyle. A considerable amount of albumen has been deposited between the ovum and the ovicapsule.

* Annal. des Scien. Nat. 1854, ii. p. 155.

cussata, according to Leydig*, the ova are arranged in aggregated pediculated groups, from which it seems probable that they are originally produced in numbers by the multiplication or division of multiple germs, somewhat in the same manner as will afterwards be stated to have been observed by Meissner among the Gordian Nematoid Worms. An albuminous layer is afterwards formed externally, and may be instrumental at last, from its increasing thickness, in separating the ovum from its pediculated attachment to the ovary. There seems therefore to be little doubt that in these Mollusca, and in a certain number of other Invertebrate animals in which the micropyle has been observed, this apparatus is produced by the remains of an original or early ovarian pedicle. In the Unio and Anodonta it is certainly not formed by the peculiar process of development from within the ovum, which has been elaborately described by Keber.† It will afterwards be shown, however, as indeed may be concluded from what has already been stated in regard to osseous fishes, that in other animals the micropyle may arise in other modes and without the early existence of the pedicle now described.

When the ova are detached by the rupture of the pedicle in the Acephala, they lie, in different stages of advancement, but all provided with the micropyle, in the general ovarian cavity. The coverings of the Acephalous ovum appear to be composed at least of two layers, of which the inner may perhaps be looked upon as the vitelline membrane, the outer as a chorion; but sufficient data have not yet been furnished to determine the homological rank of these membranes. The early connection, in a pediculated form, with the ovarian stroma might point to a different view of their nature. Leydig states that while in Unio and Anodonta the albumen is deposited within the membranes, in Venus it is added externally. The micropyle appears to be closed previous to the commencement of embryonic development.

Arthropoda.—The ova of Articulate animals might with most propriety be classed with the large-yolked group, at least as regards the ova of Insecta, Arachnida, and the higher Crustacea. In addition to the germinal vesicle and finely granular yolk-substance, they all contain a large proportion of clear or oil globules of considerable size; and the process of segmentation is generally limited to a small portion of the yolk surface. The ova of these three classes present, however, many subordinate differences in their structure and mode of production, which renders it necessary to give a short separate account of them in this place.

Insecta.—The ova of insects are more especially distinguished by the extraordinary varieties of their external form and appearance. These varieties affect, however, principally, or depend upon modifications of the external covering, chorion or shell-membrane, as it has been called. They differ also from those of most other animals in a frequent departure from the regular symmetrical form. Some are nearly hemispherical, others more oval; many are somewhat bent in an antero-posterior direction*; many present the most curious elevations and irregularities on their external surface—reticulated ridges or fringes, and depressions, tubercles, hairs or spines, or other long processes, sometimes single, at other times in numbers. These modifications of the external coverings of the eggs of Insects appear to have reference chiefly to the protection of the ova from the effects of external injury, and to serve various mechanical purposes connected with their deposition and attachment; but they are not, in most at least, attended with any important varieties in the internal structure, which, on the whole, presents considerable uniformity throughout the whole class. The ova of all insects, we shall afterwards see, are provided with one or more apertures corresponding to the micropyle.

All recent observers agree that, in the ova of Insects, in addition to the external shell-covering, there is a delicate transparent vitelline membrane. The germinal vesicle is of proportionately large size. Its macula is at first single; but in the course of the growth of the ovum it becomes multiple, or diffused as a finely granular or molecular substance throughout the vesicle.† The germinal vesicle is situated in a vitelline or germinal area composed of fine granules, in which without doubt the limited process of segmentation afterwards takes place; but fuller observations are still much required in regard to the segmentation of the yolk in insects, which has as yet been very rarely seen. The germinal vesicle appears to be burst and diffused at a comparatively early stage of the growth of the egg.

The external membrane consists in general of more than one layer of substance. The outer and inner are described as being generally more clear, dense, and homogeneous; the middle one, in some insects at least, presenting greater varieties of structure, and not unfrequently being composed of united nucleated cells. It is in these several layers of the outer membrane that the micropyle apparatus, recently discovered, is situated. The existence of a micropyle in the ova of Insects was first published by Meissner, in September, 1854‡; but the discovery appears to have been made simultaneously by Leuckart, who has given a most interesting and elaborate description of this apparatus, and of the minute structure of the membranes, in a great variety of insects, in a memoir recently published by him.§

Meissner described several varieties of the

* Müller's Archiv. 1854, p. 320.

† Hessling and Bischoff, loc. cit.

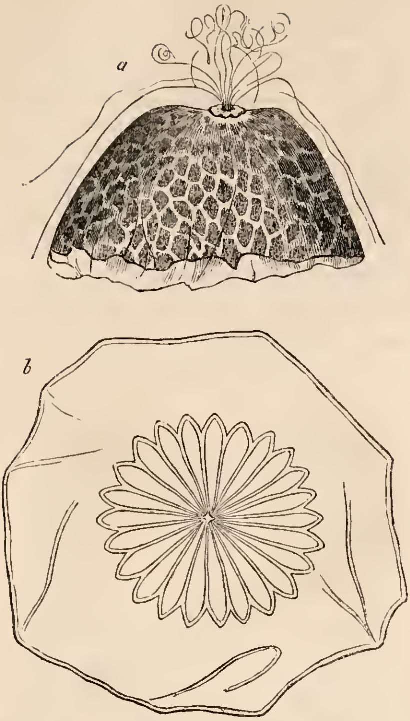
* This has reference to the position they occupy during their formation in the passages of the female parent.

† See R. Wagner's Prodromus Hist. Generat.

‡ Zeitsch. für Wissen. Zool. vol. v., p. 272.

§ Memoir on the Micropyle and Minute Structure,

Fig. 75*.



Micropyle in the ovum of Insects. (*From Meissner.*)

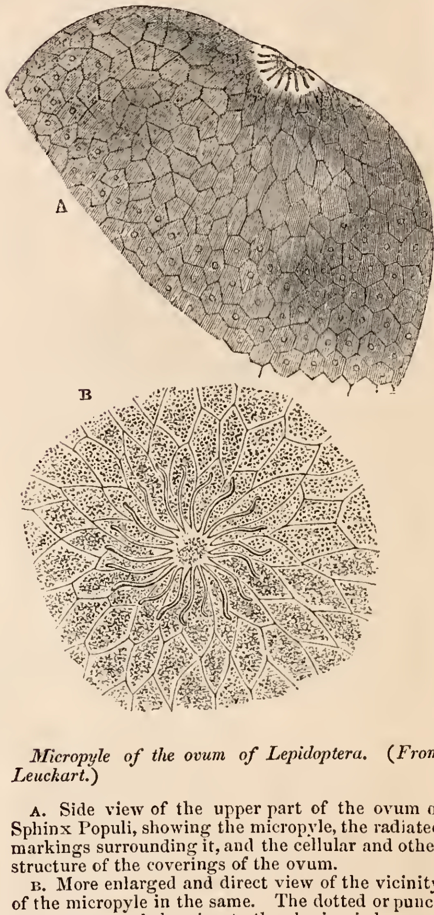
a. A portion of the upper pole of the ovum of Musca vomitoria from the Vagina. There are shown in succession the vitelline membrane, chorion and outer envelope, and at the upper part in profile the micropyle aperture situated in the middle of a nipple-like projection of the chorion, and with a number of spermatozoa involved in it.

b. Direct view of the upper pole of the ovum of an insect belonging to the Pyralida. The micropyle aperture is seen in the centre of the radiated markings of the chorion.

micropyle apparatus in the ova of Insects belonging to the following genera, viz., Musca, Tipula, Culex, Lampyris, Elater, Teleophorus, Adela, Pyralida, Tortrix, Euprepia, Liparis, Pieris, Panorpa, and in more than one species of several of these genera. The same author also observed and described in Musca vomitoria a number of spermatic filaments entangled in the micropyle.

Leuckart's observations, which are fuller and more minute than those of Meissner, and differ in some of their results from those obtained by that author, were extended over a very large number of Insects. Among nearly a thousand different kinds, he succeeded in detecting the existence of the micropyle in not less than two hundred; and his detailed observations on this apparatus, and the structure of the membranes, extend to one hundred and

Fig. 76*.



Micropyle of the ovum of Lepidoptera. (*From Leuckart.*)

A. Side view of the upper part of the ovum of Sphinx Populi, showing the micropyle, the radiated markings surrounding it, and the cellular and other structure of the coverings of the ovum.

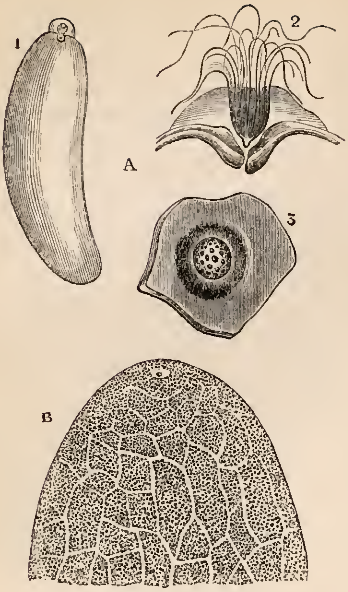
B. More enlarged and direct view of the vicinity of the micropyle in the same. The dotted or punctated structure belonging to the chorion is here represented.

eighty species. This must furnish ample proof of the universality of the existence of the micropyle in this class of animals, when we consider the minuteness of the object and the difficulty of obtaining specimens in a condition suitable for the investigation. Leuckart has stated, indeed, that in all instances in which the ova were ripe and favourable for examination, he was enabled to assure himself of the presence of this apparatus.

In a certain number of instances, amounting to about a dozen, Leuckart farther found that the spermatozoa adhere to the micropyle, and that a certain number of them pass into the ovum by this aperture. He observed that a

&c., of the Ova of Insects, chiefly pupiparous, in Müller's Archiv. Nos. 1. 2. and 3., February and July, 1855, p. 90., *et seq.*, with five plates, with 122 figures. There can be no doubt that both of these authors made the independent discovery of this curious structure. Perhaps the priority claimed by Leuckart, may be accorded to him, as he had previously stated the probability of its existence in his article "Zeugung," published in 1852, p. 906.

Fig. 77*.



Ovum and Micropyle of Dipterous Insects. (*From Leuckart.*)

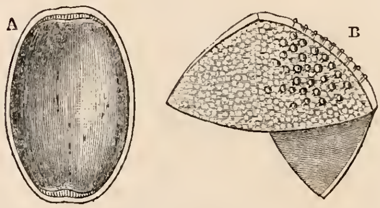
A. Ovum of Melophagus ovinus (Muscida). 1. The entire ovum, presenting at its upper part the adherent mass of spermatozoa close to the micropyle. 2. This upper part more highly magnified, showing a section of the micropyle, above which the point of the conical mass of spermatozoa glued together by an albuminous substance is inserted, while externally the filaments float free. 3. The micropyle apertures seen directly from above.

B. Side view of the upper part of the ovum of another insect of the same order, showing a single micropyle aperture and the dotted structure of the chorion.

small mass, formed of the spermatozoa which have met with the ovum in its descent through the female passage, comes to be lodged in the depression of the micropyle, and is fixed in that situation by a lid or covering of albuminous matter. It is somewhat remarkable that the greater part of this mass remains for a long time apparently without any change, even when embryonic development has advanced to a considerable extent; but he ascertained that a few of the spermatozoa belonging to the mass, usually not more than three or four, really enter the ovum and effect the change of fecundation. We are, however, as yet at a loss to conjecture what farther purpose may be served by the mass of persistent spermatozoa near the micropyle. Leuckart has also made the novel and interesting observation, that the depression and aperture of the micropyle become at a later period converted into a deeper funnel, which is connected directly with the mouth of the embryo, and undoubtedly serves, according to this author, to convey nourishment from without to the embryo. The head of the embryo lies, according to Leuckart and other observers*, in all instances, at that end or pole of the ovum which is uppermost in the oviduct, as may be most easily observed in ova of the cylindrical form, such as those of the common house-fly; but according to Leuckart, the micropyle is not, as Meissner had stated, always at that end, being sometimes at one, sometimes at the other, and occasionally at both poles. The provision for the escape of the embryo, however, is usually at the upper or anterior pole, while the lower or hinder pole more generally serves to fix the ovum, as it is often pediculated or otherwise modified in its form in connection with this purpose.

In some Insects, as is shown in the accompanying figure of the ovum in Pulex irritans, the micropyle consists of a number of foramina nearly of uniform size.

Fig. 78*.



Ovum of Pulex irritans. (*From Leuckart.*)

A. Entire ovum, magnified, showing the micropyle apparatus with a number of foramina at both poles.

B. Portion of the chorion with the micropyle foramina, more highly magnified.

In a previous part of this article allusion has already been made to the great facility with which the development of the ova of insects may be traced, in their successive stages, as they lie in different parts of the tubular ovaries and oviducts. According to the Interesting observations of R. Wagner †, the upper end of the fine ovarian tubes are filled with a number of germinal vesicles. Wagner supposed indeed that these were at first nucleoli or germinal maculæ, and that a vesicle was developed round each macula; but Leuckart‡ and Stein§ were never able to detect the germinal vesicles before they already possessed the macula. The primitive yolk arises as in most other animals—first, by the collection of a clear substance immediately round the germinal vesicle, and by the subsequent deposit in this matrix of the fine granules of the vitelline substance; later still the delicate vitelline membrane is formed, perhaps by the consolidation of a film of the primitive yolk-substance.

As the ova attain a larger size, each one being situated in the lower part of its compartment

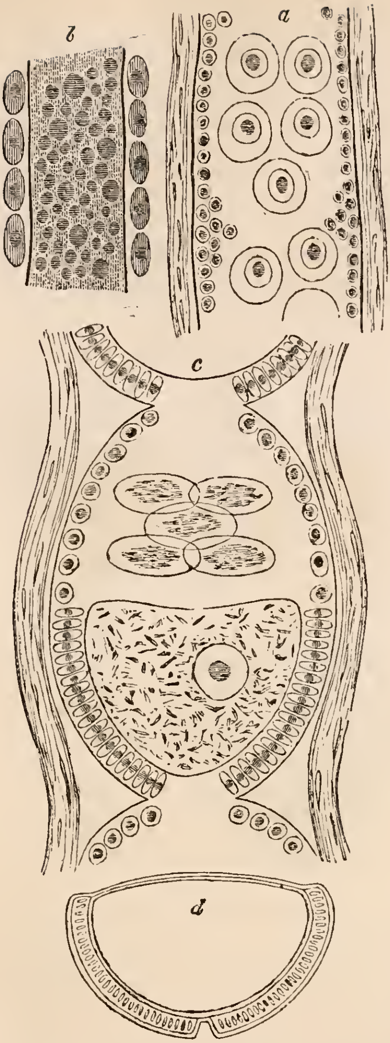
* See Kölliker, de prima Insector. Genesi, 4to. Turici, 1842.

† Prodromus, Hist. Gener. p. 9., and Beiträge zur Entwickel., &c. p. 42. See *fig.* 40. Append. of Cyclop. Anat. and Physiol.

‡ Zeugung, p. 803.

§ Vergleich. Anat. und Physiol. der Insecten, Berlin, 1847.

Fig. 79*



Development of the ova of Lepidopterous Insects. (From Hermann Meyer.)

b. A small portion of the upper part of the ovarian tube from the larva of Saturnia Carpini. The entire lines mark the basement membrane of the tube; externally elongated epithelial cells are placed on it; internally a number of larger and smaller free nuclei are imbedded in an albuminous fluid.

a. A similar portion of the ovarian tube from Bombyx Mori more developed. The external epithelial cells are visible now only as elongated nuclei; a part of the internal cells now form a lining to the wall of the tube, while others of a larger size, which have become complete cells, towards the centre, form the primitive ova; of these last only a few undergo farther development.

c. One of the loculi or chambers of the oviduct of Hyponomeuta variabilis. The wall of the tube with its external epithelial nuclei as before, enclosing now the entire loculus and the small portions of the adjacent ones represented in the figure. The lower half of the loculus is occupied by the developed hemispherical ovum in which the several parts, viz. germinal vesicle with macula, yolk and vitelline membrane, are seen. The lining cells of the oviduct are seen to be elongated and modified in structure preparatory to their forming along with the albumen one of the external coverings of the ovum (chorion). In the middle of the upper half of the loculus there are the remains of five aborted primitive ova.

d. Section of the coverings of the ovum of Harpyia vinula, which may be taken as an example of the hemispherical ovum of Lepidopterous insects.

of the oviduct, there are to be seen in the intervals between the ova numbers of large clear globules or cells, which have been supposed to furnish the materials for the growth of the ovum ; but it appears more probable that these are merely abortive ova or germinal vesicles, which, though at first similar in size and structure to those which have been farther developed, have undergone a retrograde process, and are ultimately removed by absorption.

The production of the chorion or shell membrane does not take place till the ovum has attained nearly its full size. It appears to proceed in part from the consolidation, over the whole surface, of one or more layers of albuminous fluid secreted from the wall of the oviduct. But the observations of Hermann Meyer* have shown, in an interesting manner, that a part of the outer membrane is also derived from a conversion into it of the inner cellular or epithelial lining of the oviduct, at the place where it is in closest contact with the surface of the ovum. Many of the varieties in the appearance and structure of the external covering may probably depend on the different modes of development of these cells. As to the origin of the micropyle, it does not appear to proceed, as has been supposed by Meissner, from the mere deficiency of these cells in a certain space; and it is not dependent, either, on its pre-existence in the vitelline membrane. On the contrary, according to Leuckart, it is formed in the chorion before it appears in the vitelline membrane ; and it is not in any way connected with an early pediculated condition of the ovum, which, as is well known, never at any time exists in insects.

Before leaving the history of the ovum in this class, it may be proper to make the following addition to what was stated in an earlier part of the article in reference to the remarkable modification of the reproductive process, by which, in the Aphides and several other insects, many individuals are produced without the formation of true ova, or the concurrence of the two different sexual products. The learned editor of the American translation of Von Siebold's "Comparative Anatomy of the Invertebrate Animals," Dr. Waldo Burnett, has given, at p. 464. of that work, a short statement of his own observations on the origin and mode of formation of the repeated broods or colonies of Aphides, made on a large species of that insect, viz., A.

* Zeitsch. für Wissen. Zool., vol. i. p. 190.

Caryæ, and of his views as to the nature of this process of non-sexual reproduction in general. The viviparous Aphides, according to Dr. Burnett, are neither male nor female, and do not possess, as has been supposed, any ovaries or oviducts. The new colony already begins to be visible within the body of its parent before the latter has itself been brought forth. The substance in which the new progeny takes its origin consists, at first, either of a single nucleated cell of $\frac{1}{3000}''$ in diameter, or of a small mass of these cells attached in the same place as that occupied by the ovary in the oviparous females. These masses increase in quantity, are subdivided by a kind of notching into more numerous masses ; and each of these being inclosed in a capsule, the whole come to be arranged in a continuous row or series. There is not, however, any germinal vesicle nor segmentation, as in the sexual ova ; and when development of the new insects is complete, it is by falling into the abdominal cavity, and by escaping through a genital aperture (porus genitalis) that the offspring is excluded.

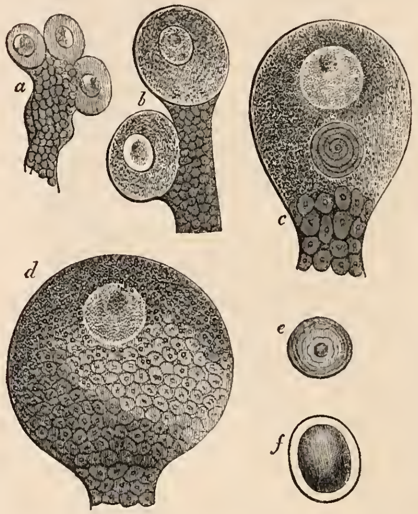
With regard to the origin of the cellular mass or germ from which the non-sexual progeny proceeds, Dr. Burnett states that a small mass, of a different appearance from the germinal part of the ovum, is seen to be included within the arches of the embryo ; and the next colony is produced from this mass. He regards this process as analogous rather to one of internal gemmation than of true generation, coinciding therefore more nearly with the views of Leuckart and Carpenter than of Steenstrup and Owen.

Arachnida.—The ova of nearly all the higher Arachnida do not differ much in their internal structure from those of Insects ; but they do not present the same varieties of external form. Their mode of first origin is also very different. All the higher Arachnida are, like Insects, of separate sexes. The Tardigrada are hermaphrodite; and in these as well as some other simpler Arachnida, as Pycnogonida and Acari, the ovum, though proportionally of large size, is of extremely simple structure, approaching very nearly to that of the lowest classes of Invertebrate animals.

The ova of the higher Arachnida are generally spheroidal ; the chorion or external membrane is generally smooth ; the vitelline membrane is slender, clear, and structureless ; the yolk-substance is not unfrequently coloured, often purplish, consisting of a considerable quantity of large oily-looking globules, smaller granules of various sizes, and larger corpuscles which have been looked upon as cells, but which Leuckart states are only aggregated masses of granules held together by a viscid substance. The germinal vesicle is proportionally large, placed eccentrically, and possesses a macula, which in some genera is simple and flattened, as in the Scorpion, in others multiple and granular, as in Epeira.

The formation of the ova may be observed in Arachnida with great ease, from the manner in which they are disposed in the ovary, projecting like bunches of grapes from the central part of that organ, in almost every stage or degree of advancement. The process has been carefully observed by Wittich * and others. So soon almost as the ovum begins to be formed, it causes a bulging or projection of the membrane from the surface of the ovary ; and when that has somewhat increased in size, the ova hang or project from the surface in small pediculated ovi-capsules. According to Wittich, V. Carus †, and Leuckart, the part of the ovum which earliest makes its appearance within the small ovicapsules is the germinal vesicle. At first it appears quite simple and without a macula, which last soon after-

Fig. 80*.



Ovarian ova of the Spider. (*From Wittich.*)

a. Small fragment of the ovary of Epeira diadema from which three ova project in the early stage of their development previous to the formation of the yolk: the germinal vesicles are enclosed in the membrane formed by the bulging out of the ovarian substance.

b. Two ova similarly situated, but more advanced ; the primitive granular yolk substance intervening between the germinal vesicle and vitelline membrane.

c. An ovum still more developed ; the germinal vesicle occupies the upper part ; in the finely granular yolk substance below is seen the dark body regarded by some as a yolk nucleus, presenting an appearance of concentric lamellar structure ; towards *c.* in the figure, or close to the connecting pedicle, the large nucleated cells are seen, which usually occupy that situation, and appear to give rise to the cellular yolk substance.

d. More advanced ovum greatly increased in bulk, the pedicle diminished, and the yolk completely occupied by the larger cells or corpuscles; the yolk nucleus has disappeared or is obscured.

e. & *f.* Different forms of the yolk nucleus or dark body, which for a variable time is placed within the ovum during its formation.

* Die Entstehung des Arachnideneies im Eierstock, &c., Müller's Archiv. for 1849, p. 113.

† Zeitsch. für Wissen. Zool., vol. ii., 1850, p. 97.

wards appears as a small dot or nucleolus. The yolk begins, in the same manner as we have had occasion to state in many other animals, first by the clear deposit of a basement substance round the germinal vesicle, and the subsequent formation of opaque granules in it; the vitelline membrane is of later formation. As the egg increases in size, the larger corpuscles and the fat globules gradually appear. The ovarian ova of several spiders contain besides the usual parts another body of a peculiar kind, the nature of which seems still involved in some doubt. This body is eccentrically placed near the yolk mass of the primitive ovum, and is of considerable size, viz. about $\frac{1}{240}''$, of a yellowish colour, and, during the earlier part of its existence at least, consisting of concentric layers of a hard granular matter. V. Carus* has compared this body to the yolk-nucleus of the Frog's ovum; and both he and Von Siebold seem disposed to consider it as in some way or other the source of the granular substance of the yolk; but according to Wittich this view is not well founded, as he has observed the body remaining in the ovum till it reaches maturity, though it loses its concentric laminated structure, and becomes clearer and vesicular. Von Siebold, on the contrary, states that it gradually disappears. The large clear or oily globules appear, according to Carus, to be produced from near the pedicle of the ovum, at a place where there is fixed a group of cells apparently destined for their formation.

No observations have as yet been made, so far as I am aware, on the existence of a micropyle in the ova of Arachnida.

Almost all the Arachnida are oviparous. The Scorpions are an exception, however, bearing their young alive; and it is deserving of notice that in this family the embryo is developed in the ovum while it still remains in the ovary. In the greater number of this class embryonic development commences in a blastoderm, which covers only a part of the surface of the yolk, situated in what may be called its lower part or pole †; and the segmentation of the yolk is therefore limited or partial, as in Insects. In the higher Arachnida the steps of this process do not appear to have been yet satisfactorily observed. I may refer, however, to the researches of Kaufmann of Lucerne on the development of the Tardigrada, as affording clear and beautiful illustrations of the process of segmentation, which is shown to be complete in the lower Arachnida.‡

Crustacea.—All the animals of this class are of distinct sex; but in the allied Cirrhipedia hermaphroditism most frequently prevails. In some of the Cirrhipedes, however, it has been shown by Mr. Darwin § that the sexes are also distinct, as in some of the species of the genera Ibla, Scalpellum, Alcippe, and Cryptophialus. In these instances the males are very minute, and are attached, almost like parasites, to certain parts of the more developed females, the place of their attachment varying in different species. It is interesting to observe that these males, as in the case of several of the Epizoa, are often of the most rudimentary organisation.*

The ova of the greater number of Crustacea, especially the more highly organised genera, belong, like those of most of the Articulata, to the group in which a considerable amount of nutritive yolk is present along with the formative part, and in which the process of segmentation in the latter is partial. The formative disc is situated on the lower surface of the ovum; and from that part the development of the embryo emanates. Even among the higher decapodous Crustacea, however, the ova are of very various sizes †; and in the lowest genera, as among the Entomostraca, the ova are proportionally the largest, although they are of the simplest structure, and present the smallest amount of nutritive yolk; so that, in this as in other classes of animals, magnitude alone is no true criterion of the internal structure of the ovum.

The ova of this class have been described principally by Rathke ‡, by Erdl §, R. Wagner ||, Leuckart ¶, Leydig **, and others; but the knowledge both of their structure and their mode of formation is yet far from being sufficiently minute or complete. They present, indeed, many varieties, which renders it difficult to give any general description of them. The following may however be stated. The ova of Crustacea are often variously and brilliantly coloured. The yolk-substance consists of a large quantity of clear globules of considerable size, having the aspect of oil globules, in which the colouring matter chiefly resides. In some ova these globules attain the size of $\frac{1}{450}$ of an inch. There is also a more fluid granular matter in the yolk, and in the more mature ova there is a layer or disc of granular corpuscles on one side which afterwards is the seat of segmentation and embryonic formation. The germinal vesicle is of considerable size, in some instances possess-

* Loc cit., p. 99.

† See the Researches of Herhold De Generat. Aranearum in Ovo, 1824; and Rathke, zur Morphol. Reisebemerkung. 1837; and in Burdach's Physiologie.

‡ Zeitsch. für Wissen. Zool., vol. iii., p. 220. See Plate vi., figs. 3. to 11.

§ Monograph of the Sub-class Cirrhipedia, &c., printed by the Ray Society, 1854, p. 27, &c.

* It is also a remarkable fact, pointed out by Mr. Darwin in his interesting Researches, that even among the hermaphrodite species there are sometimes distinct male individuals attached parasitically to the hermaphrodite animals; these have been called complementary males.

† Thus, for example, the ova of the river crawfish (Astacus fluviatilis) are twice as large as those of the common lobster.

‡ Entwickel. des Flusskrebses, 1829; in Burdach's Physiologie, vol. ii. 1837; in his Abhandl. zur Bildung und Entwickel. Gesch. &c., 1833; in Dissert. de Animal. Crustac. Generat. 1844; and various other treatises.

§ Entwickel. des Hummereies, 1843.

|| Prodrom. Hist. Generat., 1836.

¶ Article Zeugung.

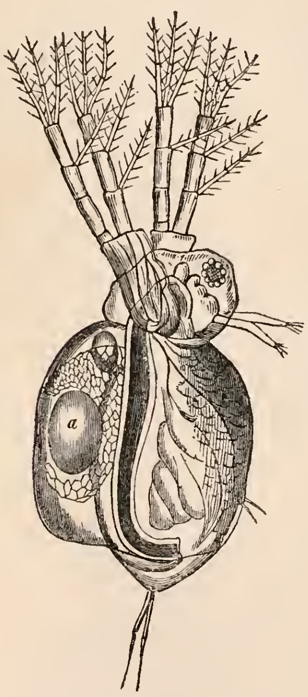
** On Argulus foliaceus in Zeitsch. für Wissen. Zool., vol. ii.

ing a single nucleus, in others multiple maculæ.

The formation of the ova may be observed with ease in any of the smaller isopodous Crustacea. According to Leuckart in Oniscus or Armadillo, it is essentially the same as in the Arachnida. The ova consist at first of germinal vesicles, originating below the epithelial lining membrane of the ovarian sac. The yolk-substance first appears as a clear deposit round each germinal vesicle; minute opaque granules are then formed in this substance, and subsequently the larger albuminous and oil globules gradually make their appearance. The vitelline membrane, which is very delicate and structureless, is added at a comparatively late period, in the Oniscus for example, when the ova are about $\frac{1}{120}''$ in diameter.

In many of the Crustacea the ova also acquire a chorion or shell membrane of considerable strength. On arriving at the lower part of the female passages, the ova of many genera also receive an addition of a peculiar so-called albuminous secretion, which becomes coagulated in water, and thus, when the eggs are laid, serves to glue them together in heaps or to cause them to adhere to the hinder feet, caudal plates, &c., of the parent, where, as is well known, they remain during the whole

Fig. 81*.



Ephippial ovum of the Daphnidæ. (*From Baird.*)

The figure represents a profile view of the female of Moina rectirostris (one of the Daphnidæ) showing at *a.* the ephippial ovum in its usual place on the back of the animal.

progress of embryonic development. In the Monoculi and some other Entomostraca, there are marsupia or pouches appended to the genital orifices of the parent, in which the ova are retained during the formation of the young.

In all the bisexual Crustacea the ova are fecundated while still within the body of the female parent; but the phenomena and period of this process have not yet been acurately determined, partly perhaps in consequence of the peculiar form and motionless condition of the spermatic corpuscles belonging to the greater number of this class. No micropyle has yet been observed in the crustacean ovum.

From the observations of several naturalists it is now well ascertained that in the entomostracous Crustacea, there commonly occurs a production of young individuals without impregnation, somewhat in the same manner as previously described in the Aphides. "In the Daphnia," says Dr. Baird *, "it is now clearly ascertained that a single copulation is sufficient, not only to fecundate the mother for life, but all her female descendants for several successive generations;" and it was considered probable by Jurine, that in some species this might extend to the fifteenth generation.

In the Daphnia and other similar Entomostraca, the ova are transferred from the ovary into a cavity situated below the shell on the back of the animal, which has been called uterus, perhaps erroneously, and there undergo development. But at certain seasons many of these Entomostraca produce ova of a different kind from those now referred to. To these the name of winter or hybernating ova has been given, as they appear to be adapted, from the strength and impermeability of their external coverings, to resist the injurious effects of cold and other atmospheric influences during the winter season. These ova are generally in smaller number than those of the ordinary kind, frequently two, sometimes only one; and they are contained and undergo development in a peculiar case, which is formed on the back of the animal below the shell, nearly in the same situation as the matrix for the ordinary ova. This case, which afterwards separates from or is abandoned by the animal, forms a sort of hump or saddle on its back, and has hence been named the ephippium, and the eggs have been called ephippial ova. These ephippial ova, according to Baird, are already fecundated by the original impregnation of the female parent, and do not require, for themselves nor for their progeny for several generations, any renewed or special impregnation.

It appears from the observations of Jurine, Strauss, and Baird, that at the time when the ephippial ova are about to be formed, a sudden change takes place in the appearance of the ova, by the deposit of a quantity of dark granular substance. This appears to be transferred

* Nat. Hist. of the British Entomostraca, Ray Soc. Public., p. 79.

into the cavity behind, in which an increased growth of substance round the ova and within the shell gives rise to the production of a two-valved case for containing the ova. According to S. Fisher of St. Petersburg *, the formation of the ephippial ova may be noticed during the whole season, from the middle of July onwards; and it may therefore be inferred that these ova have for their object the preservation of the species in the heat of summer when the ponds are liable to be dried up, as well as by resisting the cold of winter.

Von Siebold † states that these hybernating ova contain no germinal vesicle; and Dr. Burnett, in his translation of Von Siebold's work, has adduced various arguments in favour of the view that this is an instance of "internal gemmiparity" (as he regards the corresponding phenomenon in Aphides) rather than the production of true ova. Sufficient data are still wanting, however, to form a decided opinion on this subject, as we cannot at present distinguish between the ova of the Entomostraca which are the result of fecundation, and those which are formed and developed independently of the concurrence of the male.‡

Annulata.—In the class of Annulate Worms, including the Leeches, Earthworms, Nereids, and Amphitrites§, although considerable varieties present themselves in the modes of reproduction, there is yet a greater degree of uniformity in the structure of the ova than in some of the classes previously referred to.

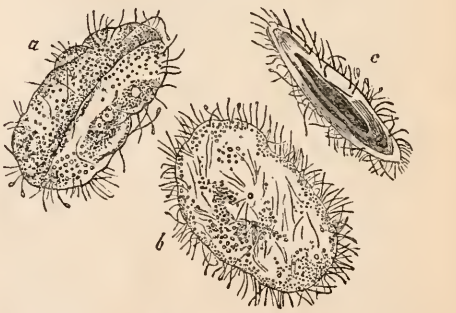
In the greater number the ova are nearly spherical in form, of rather small size; the yolk-substance is generally finely granular, and segmentation is complete; the germinal vesicle is clear, with a distinct single macula, or one which is elongated or only slightly divided into subordinate particles. In most ova of Annulata there is, in addition to the inner transparent vitelline membrane, a chorion or external membrane of considerable strength, and not unfrequently a superadded layer of albuminous substance, which unites the ova in groups or cocoons, or serves to attach them to other bodies. ‖

In Clepsine, among the Hirudinea, the yolk-substance differs from the common form above described, being composed rather of larger-sized globules; and in another genus belonging to the same order, Piscicola, according to Leydig ¶, there are peculiarities of structure which have not as yet been referred to any general law. In the ova of these animals the covering is double, consisting of a delicate internal vitelline membrane, and an external envelope or chorion, to which a layer of distinct flattened and nucleated cells is adherent; and within the vitelline membrane there is a collection of nucleated cells which displace and partially surround the usual finely granular or formative yolk-substance. Leuckart* informs us that the same peculiarity exists in Pontobdella; but the nature and destination of this inner cellular part of the ovum does not appear as yet to be understood in either of the animals mentioned.

In the Piscicola, Leydig observed the ovum, while within the ovarian cavity, to be completely surrounded for a time and enclosed by a consistent mass or covering of spermatozoa; and it has been observed that in this animal the germinal vesicle has not in general disappeared till some time after the ovum has thus encountered and been enveloped by the mass of spermatic substance.

In the Lumbricus, Meissner † has made the novel and interesting observation, that previous to the encounter of the spermatozoa with the ovum, the latter loses the vitelline membrane which before covered it, and that the spermatozoa then penetrate, in great numbers, the whole surface of the exposed yolk.

Fig. 82*.



Ova of the Lumbricus during fecundation. (*From Meissner.*)

The figures represent three views of the ova of Lumbricus agricola, *a.* & *b.* on their flat sides, *c.* seen edgeways. Over the surface spermatozoa are seen penetrating the vitelline substance, giving to it on a large scale the appearance of a ciliated surface. The ovum which has now reached the receptaculum seminis is without vitelline membrane, the yolk being thus directly exposed to the action of the spermatic masses; but the vitelline membrane existed at an earlier period and disappeared by solution in the course of the descent of the ovum.

The development of the ova in Hermella has been minutely described by Quatrefages; and this may be taken as an example of the general nature of this process among the

* Mem. of the St. Petersburg Acad., 1848, tom. vi., p. 162.

† Compar. Anat.

‡ See Burnett, loc. cit., p. 353; Zencker, über die Daphnoidæ in Müller's Archiv., 1851, p. 112; and Leydig, über Artemia salina und Branchipus stagnalis, in Zeitsch. für Wissen. Zool., vol. iii. 1851, p. 297.

§ Suctoria, terricola, errantia, and tubicola.

‖ For a clear and comprehensive account of the reproduction of the Annelida in general, and with special reference to the genus Hermella, one of the suctorial Annulata, the excellent memoir of Quatrefages, in the Annal. des Scien. Nat., 1848, vol. x. p. 153, in which, in addition to his own researches, are duly recorded those of previous observers.

¶ Zeitsch. für Wissen. Zool., vol. i. p. 123.

* Article Zeugung, p. 809.

† On the penetration of spermatozoa, &c., in Zeitsch. für Wissen. Zool. vol. vi.

Annelida. According to this description, the first germs of the ova consist of minute germinal vesicles formed in the ovarian substance; they soon acquire the single macula or nucleus. After undergoing some enlargement, these germs fall into the abdominal cavity, and there acquire, by deposit round them, the clear primitive vitelline substance. In this substance opaque granules, which are at first colourless, are subsequently deposited; and as these extend outwards from the germinal vesicle, and accumulate in quantity so as to increase the bulk of the whole ovum, a delicate vitelline membrane is added externally. The germinal vesicle attains a diameter of about $\frac{1}{950}''$, and its macula of $\frac{1}{2500}''$; and when the several parts of the ovum which have been mentioned have appeared, and the yolk is now coloured, the whole ovum has a diameter of about $\frac{1}{330}''$.

The superficial part of the yolk consists of minute coloured granules. Within this there are larger oil-like globules free of colour, and in the innermost part a somewhat viscous transparent fluid.*

According to Leydig, the germinal vesicle in Piscicola becomes enveloped by a second vesicle or cell-wall before the formation of the yolk-substance; but it is suggested by Leuckart that he may have been misled in this by the appearance often presented by the clear and somewhat highly refracting substance which in many animals precedes the formation of the opaque yolk. If this is not so, the fact observed by Leydig would constitute a marked departure from the usual homological relations of the ovum.†

Rotifera. — Although most zoologists are now disposed, on the ground of the analogies in the most important parts of their general structure, to place the Rotifera among or close to the Articulate Worms, yet in some respects their mode of reproduction presents a marked correspondence with that of the lower Crustacea. Thus they have, in common with some of the lower Crustacea, the occasional separate condition of the sexes, the preponderance of females, the imperfect development of the males, the proportionally large size of the ova, and the production of winter ova as well as the ordinary kind; on the other hand, the simpler structure of the ovum and its complete segmentation are more similar to what is observed among the Vermes.‡

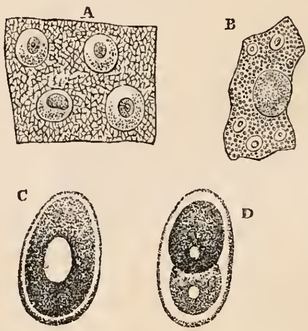
* Quatrefages, it is to be observed, designates the enveloping membrane ovarian and not vitelline membrane, which last he holds is wanting in these ova.

† Farther interesting views of the ova of this class will be found in Milne Edward's memoir in the Annal. des Scien. Nat. for 1845, vol. xxiii. p. 145; and in his article ANNELIDA in this Cyclopædia, to which I must refer the reader; in Grube's Untersuch, über die Entwickel. der Clepsine, Königsberg, 1844. H. Koch, Ein Worte zur Entwick. von Eunice, with an Appendix by Kölliker, on Exogone and Cystonereis.

‡ See Leydig, On the Structure and Systematic Position of the Rotifera, &c., in Zeitsch. für Wissen. Zool., vol. vi.; and C. Vogt on the same subject in vol. vii. of the same work.

The relation of the sexes in Rotifera has only recently been in any degree understood, and that only in a few genera; and there are still many points requiring elucidation. The greater number of the animals, in fact, which till lately have been known or described in this class have been females; and as yet the males or male organs have been ascertained only in a few genera. Some are certainly of separate sexes, as Notommata, and the allied Rotifer of which the male was first discovered by Brightwell*, and of which the development was described by Dalrymple†, Others seem to be hermaphrodite, as in Megalotrocha, described by Kölliker‡; in Euchlanis, by Schmidt§; and in Lacinularia socialis, by Leydig.‖ But according to Huxley¶, there may still be some doubts as to the bodies described as spermatozoa, and as to the arrangement of the male organs in the Lacinularia.

Fig. 83*.



Ovarian ova of Rotifera. (*From Huxley.*)

The figures represent the formation and development of the true or ovarian ova of Lacinularia socialis (one of the Rotifera). A. and B. are small fragments of the ovarian substance showing the primitive ova with their germinal vesicles and maculæ; in B. one of the ova more advanced than the rest. C. represents the mature ovum. D. the same undergoing the first stage of segmentation.

The ova of Rotifera have been observed by Ehrenberg and many other microscopists. They are of comparatively large size, but yet belong to the group of ova possessing the simpler kind of structure, the yolk substance being quite finely granular, and undergoing a complete segmentation. The germinal vesicle is large, and possesses a distinct single macula; and the whole ovum is inclosed in a clear vitelline membrane. No micropyle has yet been discovered, nor have the time and

* Ann. of Nat. Hist. for Sept. 1848, p. 153.

† Philos. Transact., 1849, p. 331.

‡ Froriep's Neue Notizen, 1843, p. 17.

§ Vergleich. Anat. p. 268.

‖ Zeitsch. für Wissen. Zool., vol. iii.

¶ Microscop. Soc. Trans. p. 1. in vol. i. of Microsc. Journal, 1853.

phenomena of fecundation been minutely observed.

The formation of these ova may be traced with facility in the substance of the ovary, in consequence of the transparency of the animals. The nucleated germinal vesicle seems first to make its appearance; the granular yolk substance follows; and the vitelline membrane is last formed.*

The Rotifera present another example of the formation in the autumn season or before winter, of that variety of the reproductive body which has been called winter egg, and which has already been noticed under the Entomostraca. These bodies were observed by Ehrenberg in Hydatina and Brachionus, by Dalrymple in Notommata, and by Huxley and Leydig in Lacinularia. They are twice the size of the ordinary ova, are formed in very small numbers, probably only two, as is most common in Daphnia, and contain no apparent germinal vesicle. Mr. Huxley† appears to have pointed out very clearly the distinction between true or ordinary ova and these reproductive bodies. He says, at p. 16 of his paper, "The true ova are single cells which have undergone a special development, the ephippial ova are aggregations of cells, in fact larger or smaller portions, sometimes the whole of the ovary, which become enveloped in a shell and simulate true ova." Mr. Huxley

Fig. 84*.

Formation of *Ephippial ovum in Lacinularia Socialis.* (*From Huxley.*)

A. represents a portion of the ovary massed together and undergoing a change of structure preparatory to its conversion into the ephippial ovum.

B. the ovum now complete, the external investment distinct.

C. the same having now its contents divided into two portions. The ephippial ova differ from the ordinary ones in their mode of formation, and in having three investments.

has traced minutely the process of conversion of the substance of the ovary into such an ephippial ovum, or rather the protecting covering of the two ova which are contained in the ephippium; and his observations seem to show a manifest difference between these and the ordinary ova. The same follows also from Mr. Dalrymple's researches on Notommata. The correspondence of the number and general structure of these ova in Daphnia and the Rotifera is also deserving of notice. These winter ova, besides being much larger than the ordinary ones, differ from them also in structure, having three investing membranes; and they appear designed, like those of the same kind in other animals, to resist the cold of winter and other hurtful influences.

It would appear that these ephipphial ova, like those of Daphnia, do not require fecundation. Leydig, though distinguishing the two kinds of ova, regards the hybernating ova as only modifications of the ordinary ones; while Huxley considers them rather as peculiar buds like those of Aphis or Gyrodactylus.*

Turbellaria.—Under this class three orders of the animals allied to the Planaria may be brought, according to the researches of Quatrefages and others, viz., the two kinds of Planaria with simple and ramified alimentary canal, or Rhabdocœla and Dendrocœla, and the Nemertides or Miocœla. The first two orders are hermaphrodite; in the third the sexes are distinct. The ovology of this class is known principally from the interesting and beautiful researches of Quatrefages †; but the history of the structure and formation of the ova is still far from being complete.

The ova of the Planariæ are of various magnitudes, and present some differences in their structure. For the most part they contain only the finely granular yolk, but with occasionally some oil globules interspersed. It is only in the earliest stages that the germinal vesicle is perceived with ease, in consequence, probably, of the opacity of the yolk-substance, and the dark colour of the external envelopes.

In most of the genera the germinal vesicles and the yolks are formed in separate organs, as in the trematode animals, to which the Planariæ are nearly allied, but in some, as Macrostomum, these two organs come to be combined in one. At first the yolk-mass, in descending and meeting with the germinal vesicles, unites a number of them into a connected chain; but somewhat later the ova are separated into distinct spheres, and a vitelline membrane is formed to enclose each of them.

Just as occurs in the body of the adult Planariæ, there is also in the ova a remarkable tendency to subdivision by fission. Thus, in the commencement of the development of the ovum, it is liable to become divided into distinct masses, so as to give rise to the development of a number of embryoes from one ovum. Such, at least, is the view entertained by some; but there may be doubts as to whether the ovum so divided is really simple,

* Leuckart, loc. cit.
† Loc. cit.

* See on this subject also, Burnett's translation of Von Siebold's Comparative Anatomy, p. 150.

† Mém. sur quelques Planariées Marines, in Annal. des Scien. Nat. 1845, tom. iv. p. 169; and Mém. sur la Famille des Nemertiens (Nemertea), id. lib. 1846, tom. vi., p. 269. The Rhabdocœla are known chiefly by the researches of Schmidt, Die Rhabdocœlen Strudelwürmer des süssen Wassers, Jena, 1848; and of Schultz, Beiträge zur Geschichte der Turbellarien, 1851.

or is rather a collection or aggregation of a number of germs surrounded by a common yolk; in fact, as has been suggested, an ovarian sac containing a number of ova.*

The manner in which the spermatozoa reach the ova for fecundation does not appear to have been ascertained with accuracy.

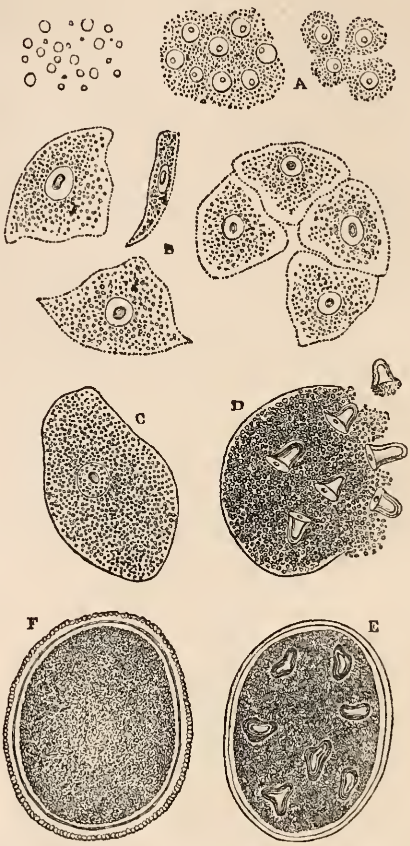
Entozoa.—The ovology of the Helmintha or Entozoa has received considerable attention from physiologists, both on account of the interesting nature of the phenomena presented by its study, and because of the anxiety to discover the mode of production of these parasites within the bodies of other animals. From the researches on this subject which have been prosecuted with great assiduity by a number of observers in recent times, not only have many doubtful points been solved as to the origin of the Entozoa, and the views of naturalists greatly modified in regard to the history of these animals, but considerable assistance has also been received in the elucidation of general questions in ovology. I will give a short sketch of what has been most recently ascertained on this subject under the three divisions of the Nematoidea, including all the Round Worms, the Trematoda, and the Cestoidea including the Cystica. All the animals belonging to the first division are bisexual, and the production of the embryo is direct from the ovum, without metagenesis or metamorphosis; in the two other divisions hermaphroditism prevails, and development is indirect, or accompanied by metagenesis and metamorphosis in the greater number.

Nematoidea.—The genital organs in the first of these orders present the same favourable circumstances as those of Insects for the observation of the structure and formation of the reproductive elements in their successive stages, as in the different parts of these tubular organs there are to be found at once the spermatic cells and spermatozoa, and the germinal cells and ova in every conceivable degree of advancement from their earliest apparition to the state of maturity.

In the Ascarides and most of the round worms, the upper closed extremities of the two genital tubes of the female correspond with an ovary, or rather as a portion of it which may be regarded as a germ-forming organ; for in this upper part of the tube are produced only the nuclei or nucleated cells, from which the germinal vesicles derive their origin. A second portion of the tube, in which the granular yolk substance is added, is to be looked upon also as a constituent part of the ovary, and may be called the yolk-forming or vitelligenous organ. Next follows a constricted part of the tube, which may be termed oviduct, in which the ova meet with the spermatic corpuscles and undergo fecundation. From this the ova pass into the fourth compartment, a dilated portion which has been called a uterus, and below this the two genital tubes finally unite into a common vagina.

In the Ascarides, the process of formation

Fig. 85*.



Development and fecundation of the ova of Ascaris mystax.

A. Earliest stage of the ova as they are found in the cœcal or uppermost part of the ovarian tube; some from the highest part are mere molecules, others a little farther down are minute nucleated cells (germinal vesicles or germs of the ova), and round these the primary yolk granules are beginning to collect.

B. Ova from the second part of the ovarian tube in which they are closely pressed together and arranged in a radiated manner round the axis or centre of the tube. To the right, four of these ova are represented adhering together; to the left, two ova are shown with their flat surfaces, and one with its thin edge towards the observer. The external dotted line represents the surface of the basement substance of the yolk in which the opaque vitelline granules are deposited; there is as yet no vitelline membrane; the germinal vesicle and macula are very distinct.

C. An ovum from the oviduct; a faint marginal line indicates the place where the vitelline membrane is afterwards formed. The germinal vesicle still visible, though obscured by the yolk granules; the ovum has now assumed an ovoid shape.

D. Softened state of the ovum at a slightly later stage, when it has met with the spermatic cor-

* Burnett's transl. of Siebold's Compar. Anat. p. 140.

puscles; which are held by Nelson thus to penetrate or gain access to the vitelline substance.

E. Ovum more advanced; the vitelline and albuminous membranes formed; clear highly refracting spaces resembling altered spermatic corpuscles are seen in the yolk substance.

F. Ovum after fecundation; uniform structure of the yolk substance previous to the appearance of the embryonic cell and commencement of segmentation. The chorion has now become tuberculated.

of the ova appears to consist, first, in the production of minute cell-germs in the uppermost part of the ovarian tube immediately adjoining its cœcal termination. It does not appear to be fully ascertained whether these germs are originally, as some have supposed, the maculæ or nuclei, or rather, as others hold, the germinal cells or vesicles themselves: the latter opinion appears to be the most probable. Second, the granules of the yolk-substance very soon collect round the exterior of the germinal vesicles. These granules appear at first to be suspended in fluid; but a little later, as they come to collect round the germinal vesicles, they are united together in a mass by a firmer but clear basement substance, and when the minute ova have somewhat increased in size, the outline of this clearer basement substance of the yolk is distinguishable. There is not, however, at first any external or vitelline membrane; of this Dr. Nelson and I have convinced ourselves by repeated observations in Ascaris mystax.*

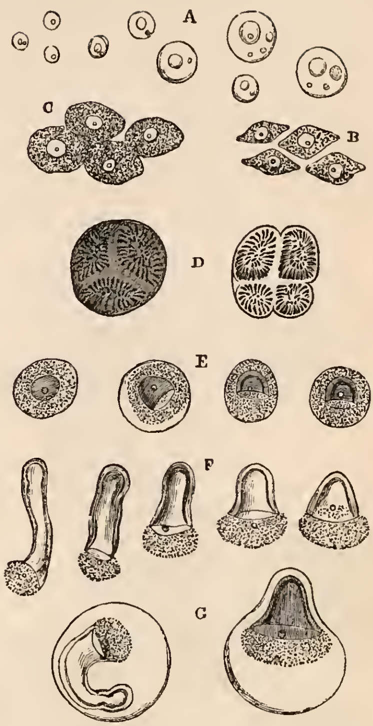
The ova, as they continue to descend in the vitelligenous part of the tube in immense numbers closely pressed together, assume the form of subtriangular flattened bodies, and come to be arranged in series of three, four, or more, in a short spiral round the centre of that part of the ovarian tube which constitutes the yolk organ, as round a central axis, but without being united together by any common stalk or other structure. A prodigious number of ova are thus packed together in a very small space.

In passing through the next part of tube, which forms an oviduct, the ova are detached from the spiral and closely-set position, and being surrounded by fluid, which must here be secreted within the tube, descend one by one through its narrower part. At this place they encounter the spermatic corpuscles when they are present, and undergo the change of fecundation; but whether fecundated or not, the ova now lose their germinal vesicles, alter their form from that of flattened triangles to oval, become for a time much more yielding and soft, and somewhat later begin to acquire an external covering which they have not previously possessed.

The peculiar motionless and tailless spermatic corpuscles appear, therefore, to come into contact with the ova when the yolk is exposed directly to their action. According to the interesting observations of Dr. Henry

* See Nelson's paper on the Reproduction of the Ascaris Mystax in the Trans. Roy Soc. of Lond. 1852, p. 563., pl. 28, figs. 48. and 50.

Fig. 86*.



Development of Spermatic Corpuscles in Ascaris mystax.

This figure is introduced to show the several stages of development of the peculiar acaudal and motionless spermatic corpuscles of the Ascaris mystax.

A. shows various stages of the primary sperm-cells or rather sperm-germs; in the more advanced of which towards the right, internal cells are seen forming by endogenous production within the primary germ-cells.

B. & C. show the second stage, in which the separated germ-cells have each become covered by a finely granular mass collected round them; in B. this process is beginning; in C. it is completed, and the sperm cells thus formed have assumed an ovoid shape.

D. Two views of sperm-cells in the third stage, in which a quadrifid division of the whole cell has taken place preparatory to the escape or separation of the spermatozoon-cells, usually four in number, proceeding from each sperm-cell.

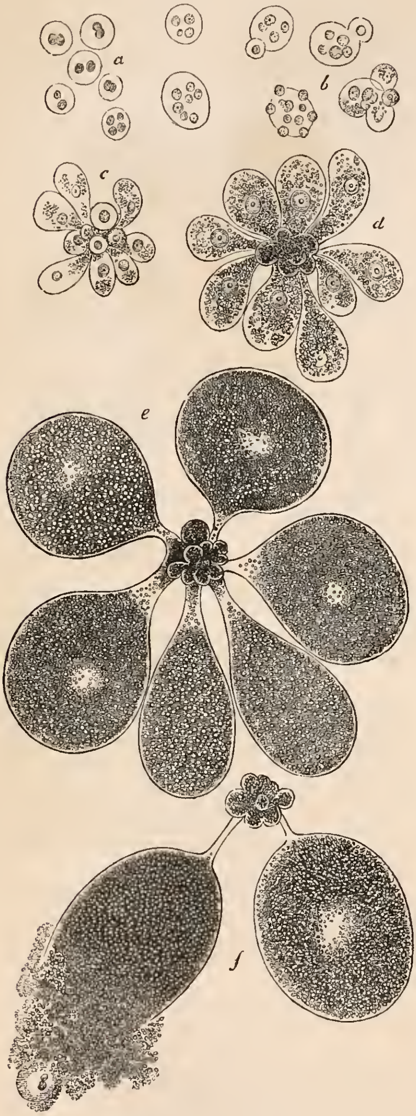
E. Various views of these spermatozoon cells in which the radiated linear marking (seen in D.) has disappeared, and is again resolved into granules; the nucleus is seen from above in the left-hand figure; in the three others being viewed in profile the appearance of the bell-shaped spermatic corpuscle with the nucleolus is perceptible.

F. Exhibits from right to left the various progressive stages of the bell-shaped corpuscle into the test tube form; the remains of the nucleolus and granular substance are seen towards the mouth of the flask-shaped bodies.

G. Illustrates the effect of water in developing "Sarcode" on the exterior of these corpuscles in two different stages of their advancement.

Nelson,* a peculiar softening of the ova, which may be caused by the rapid imbibition of fluid at the time the changes above mentioned are taking place, renders them peculiarly liable to be impressed by the spermatic corpuscles at

Fig. 87*.



Development of ova in Mermis albicans, belonging to the Gordiacei. (*From Meissner.*)

a. Germ-cells from the upper or cœcal end of the ovarian tube, their nuclei undergoing subdivision.

b. Various stages of farther multiplication of the internal cells, which in the more advanced are seen to approach the surface of the original cell, and to cause the bulging of its membrane by the enlargement of the internal cells, which last constitute the primitive ova.

c. & d. Groups of primitive ova thus formed; some of them much more developed than others, presenting internally the nucleated germinal vesicles and yolk granules and attached in pediculated capsules, which are formed by the extension of the membrane of the primary germ cells.

e. A group of these ova more advanced; the opaque granular yolk increased in quantity so as to obscure in part the germinal vesicles; the pedicles much narrowed and somewhat elongated; the external ova are nearly mature; those in the centre remain abortive.

f. Two similar ova now ripe, a part of one of them is artificially burst, showing the escape of the yolk granules and germinal vesicle with a double macula. The remains of the pedicles when detached from the central mass constitute, according to Meissner, the micropyle aperture.

this period; and Nelson is of opinion that these corpuscles even penetrate completely into the yolk-substance, and ultimately combine with it. Little doubt can be entertained that a combination of the spermatic and vitelline elements in some manner takes place at this time, whether by the direct interpenetration after the mode described by Nelson, some may be inclined to doubt; but at all events the spermatozoa act immediately on the vitelline substance at this stage of the progress of the ovum. *

As the ovum descends in the next part of the tube or uterus, the external membrane becomes more dense, additional layers are deposited upon it, and at last it acquires more

* Loc. cit., p. 576.

* Professor Bischoff has, in his recently published tract "Wiederlegung des von Dr. Keber bei den Naiaden und Dr. Nelson bei den Ascariden behaupteten Eindringens der Spermatozoiden in das Ei," &c., Giessen, 4to., 1854, called in question the accuracy of Nelson's observations, and asserted that Nelson's spermatozoa are only epithelial particles belonging to the female passages. In a subsequently published paper, entitled, "Bestätigung des von Dr. Newport bei den Batrachiern und Dr. Barry bei den Kaninchen behaupteten Eindringens der Spermatozoiden in das Ei, Giessen, 25th March, 1854," although Bischoff has seen reason to alter his previous views as to the phenomena of fecundation in the Ascaris mystax, he still in that paper, and in a special memoir on the subject, published in the Zeitsch. für Wissensch. Zool., 1854, vol. vi. p. 377. adheres to the view that the bodies which I, along with Nelson and Meissner, regard as spermatozoa are no more than epithelial cells. I have elsewhere shown that this view is altogether untenable, and that no doubt can now prevail as to the corpuscles in question being the product of development from the spermatic cells of the male Ascaris, and as to the possibility of their direct action on the ova within the female previous to the formation of the vitelline membrane. Meissner has also given the most satisfactory evidence on the same point in his memoir on the penetration of the spermatozoa into the ova of animals, contained in the same volume of the last quoted work, though this author takes a different view from Nelson and myself as to the manner in which the spermatozoa are admitted into the ovum in Ascaris mystax, believing in the existence of a vitelline membrane and micropyle, in the same manner as in Mermis and other Gordiacei, which he has so well described. With regard to this view as applied to the Ascaris mystax, Bischoff's observations, Nelson's, and my own, give me the greatest confidence in asserting that there is at first no vitelline membrane in this animal at the time when the ova first meet with the spermatic corpuscles.

or less of a minutely tuberculated structure on its external surface. The ovum becomes of a regular short oval or nearly spherical form. If fecundation shall have occurred, the embryonic vesicle or cell makes its appearance, and the phenomena of segmentation follow in rapid succession.

Fig. 88*.

Formation and fecundation of the ova of Nematoid Worms. (According to Meissner.)

a. A portion of the ovarian axis and early ova attached to it from the ovarian tube of Strongylus armatus. The axis column occupies the centre of the tube, and the ova are suspended to it by pedicles, supposed by Meissner to form micropyle apertures when they are detached.

b. View given by Meissner of a set of the nearly ripe ova of Ascaris mystax, which he conceives are thus connected by pedicles to a central axis.

c. Two mature ova of the same surrounded and in part penetrated by spermatic corpuscles. At the narrow angles of these ova a spermatozoon is seen passing into the interior by what Meissner has regarded as a micropyle formed by the detached pedicle. In the ovum to the right a spermatic corpuscle is seen in the vitelline substance. The existence of such a micropyle aperture and pediculated attachment of the ova in the Ascarides I regard as doubtful.

In others of the Nematoid Worms and more especially in Strongylus and the Gordiacei, it would appear from the researches of Meissner, that the first germs of ova which take origin in the uppermost part of the ovarian tube multiply by an endogenous production, and that in this manner groups or bunches of the primitive ova are produced which are connected together by pedicles arising from the

Fig. 89*.

Formation of ova and fecundation in Gordius Subbifurcus. (From Meissner.)

a. A small portion of the ovarian tube with groups of the ova partly within and partly escaping from it.

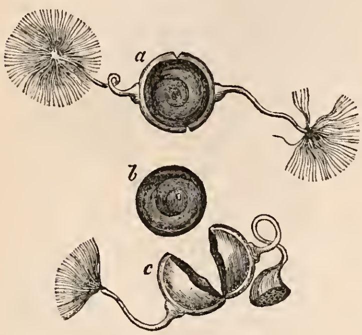
b. Three of the mature ova from the lower part of the oviduct surrounded by the spermatozoa. The ova are now isolated, and the pedicle of each is open, and is regarded by Meissner as a micropyle, by which spermatozoa, as represented in two of them, enter the ova. The germinal vesicle is still to be seen.

elongated membrane of the original germ-cell which remains as a covering of the whole. A certain number of these ova make progress in development while others probably become abortive. As the ova enlarge they are more spread out in the tube and take something of the spiral disposition which exists in the Ascarides, but with this difference, as already noted, that the various ova remain connected together by the attachment of their pedicles to a central axis or stem running down the middle of the ovarian tube. On the subsequent detachment of the ova by the breaking of these pedicles, according to Meissner, a micropyle aperture is formed in each ovum for the admission of the spermatozoa. The accompanying drawings from Meissner's Memoir will give a sufficiently clear idea of his views on this subject.

The ova of the nematoid worms constitute a marked example of the simpler kind of ovum in which the formative yolk is present, and in most but not in all of which segmentation is complete. This process was first made known through the interesting researches of Kölliker *, in Müller's Archiv., 1843, p. 68, and Bagge, in his Inaugural Dissertation.† The memoir of Reichert in Müller's Archiv., 1847, contains very correct views as to the formation of the spermatic cells.

The accompanying figure from Meissner‡, gives a representation of a remarkable form of the external capsule of the ova occurring in some of the Gordiacei (Mermis nigrescens).

Fig. 90*.



Mature ova of Mermis nigrescens. (*From Meissner.*)

This figure is introduced to show the very peculiar capsule in which the ovum is enclosed.

a. Ovum taken from the uterus with embryo enclosed; the chorion and shell capsule with chalazæ or brush-like processes attached to the latter.

b, c. The shell capsule *c* burst across the equatorial groove, allows the ovum *b* to escape with the chorion and embryo contained within it.

The ova of Trematoda are generally of a long-oval form, and of middle size. They are enveloped by a shell membrane of considerable firmness, and which is not unfrequently of a dark brown colour. The yolk-substance contains fat corpuscles simple and compound; and there is a germinal vesicle present, which, however, from the deep colouration and other circumstances, is often very difficult of detection.

In these animals an interesting peculiarity in the arrangement of the reproductive organs exists, in the separation of the germ-forming and yolk-forming portions from each other; in the first of these organs germinal vesicles or clear nucleated cells alone being produced, in the other the opaque granular fatty matter which furnishes the vitellus. This arrangement was first described by Von Siebold in 1836.§ The germ organ is generally in the form of a rounded sac, which is filled with the nucleated germ-cells or vesicles in various stages of development. The vitelline organ is double, each one consisting of cœcal tubes, in which the opaque granular yolk-substance is secreted.* The ducts of these two organs meet in a common cavity or uterus, and the germs descending into this cavity are there enveloped by a portion of the vitelline mass, and shortly afterwards an enclosing vitelline membrane is formed. These animals being hermaphrodite, the vas deferens of the male organ or testicle leads into the uterine cavity; and it would appear, therefore, that in many cases, if not in all, impregnation takes place by the access of the spermatic corpuscles to the elements of the yolk and germinal vesicle, just at the time when they are brought together to form the ovum.

This separation of the germ-forming and yolk-forming parts of the ovarian organ, which is so apparent in the Trematoda, is not in truth so great a departure from the more familiar structure of other animals as might at first be thought; for, as Leuckart has well observed, there are other examples of the same disposition, or an approach to it. Thus in Insects and in Nematoid Worms, as we have seen, it is from distinct parts of the genital tube that the germs and yolk are produced; and more or less of the same arrangement exists in all instances in which the form of the ovary is tubular.

The Cestoidea present a great similarity to the Trematoda in the arrangement of the organs by which the ovum is formed. Indeed, notwithstanding the difference of their antecedent stages of development, the structure of the mature sexual joint or proglottis of the tapeworm, offers so great a resemblance to that of some of the Trematoda, that they have been regarded as identical by several recent observers. In each sexual joint of the tapeworm, the testicle and the two parts of the ovarian organ coexist, and, as stated in an earlier part of this article, arrive at maturity simultaneously in the posterior or oldest segments of the body. Van Beneden has, in his recent work on the Cestoid Worms†, described very clearly the structure and relations of the germigenous and vitelligenous parts of the eproductive organs in the complete segments or proglottides of a variety of Cestoid worms. The ova originate in the first mentioned of these organs as germinal vesicles, and, passing into the vitelligenous part, meet with the yolk-masses formed there. Near the same place is situated the seminal vesicle, from which, doubtless, the spermatic substance easily reaches the ovum as it descends in the course of its formation. The ova then acquire an external envelope, and pass into the cavity termed a uterus. As they come to be accumulated in gradually increasing quantity in the latter cavity, they distend it to a great degree, so as to cause it to pervade in various forms, ramified and others, the whole body of

* See his admirable memoir on the first changes in the fecundated ovum, principally referring to the Entozoa.

† Dissert. inaug. de Evolutione Strongyli auricularis et Ascaridis acuminatæ, Erlangae, 1841.

‡ Zeitsch. für Wissen. Zool. vii. pl. ii.

§ Wiegmann's Archiv., 1836, p. 217, Tafl. vi., and Müller's Archiv. 1836, p. 232, Tafl. x., fig. 1.

* See also Thaer on this subject, in Müller's Archiv., 1850, p. 626.

† Mém. sur les Vers Cestoides. Acad. Roy. de Belgique, tom. xxv. 1850, see plate B.

the proglottis; and finally they are discharged from this, usually after the separation of the joint from the main tapeworm, by the irregular rupture of the outer wall, or by a genital aperture. Here, then, we have another instance of the combination of the several component elements of the ovum together with the sperm, previous to the enclosure of the whole by a membrane so as to give the form of a complete ovum.

The ova of most of the Cestoidea, as in the common tapeworms, are of proportionally small size. The external envelope is firm, thick, and nearly homogeneous; sometimes, however, presenting a slight appearance of fine radiated striæ passing through it, which recalls the structure of the thick membrane of the Fish's ovum. The vitelline substance is very finely granular, or almost clear; the germinal vesicle is perceived with difficulty, but is of large size.* In some Cestoids the external envelope is of a brown colour, as in the Trematoda, and in others presents peculiar forms and prolongations from its surface. A delicate vitelline membrane is described within the outer covering by some authors.†

The segmentation of the yolk appears to be complete; but this process has been observed only in a few instances.

Of the ova of the Cystic Entozoa nothing need here be said, seeing that it has already been shown that the several genera of this order, viz., Cysticercus, Cœnurus, and Echinococcus, are only larval and aberrant forms of the Cestoid worms, and being immature animals, never produce ova, excepting through their more advanced stage of cestoid development.

Echinodermata. — The different orders and families of this class are all of distinct sex, so far as is yet known, with the single exception of one of the Holothurida, viz., Synapta (S. Duvernæa), described by Quatrefages‡ as presenting a combination of the testicles and ovaries in one organ, resembling in some measure that which exists in the Gasteropodous Mollusca.

In the females of Echinus, Asterias, and Holothuria, the ova have been studied with care by different observers. In all of them the ova present, when mature, more or less of a deep yellow, orange, or red colour, which belongs to the yolk-substance. This substance is finely granular, and is enclosed, at least in some, as Echinus, by a delicate vitelline membrane; but in others, as Holothuria, there is a considerable deposit of an albuminous layer of a peculiar structure, which, from its adhering closely to the vitelline membrane, obscures the latter envelope, and thus has made its existence doubtful to some observers. This albuminous deposit also exists in Echinus, but is in that animal distinguishable from the vitelline membrane.*

The colour and opacity of the yolk-substance in the mature state of the ovum usually prevent our perceiving the germinal vesicle; but in the earlier stages of formation, when the ovum is of lighter colour or even quite clear and transparent, a germinal vesicle with a single distinct macula is easily perceived. This vesicle has disappeared in the ova which are deposited. The segmentation of the yolk is complete in the Echinodermata: the process has been fully traced by Sars in Asterias†, and by various observers in some other genera.

It was in the ovum of Holothuria tubulosa that Professor Johannes Müller first made the novel and interesting discovery of an aperture leading through the thick external membrane towards the yolk; an observation which has been confirmed by various other physiologists‡, and has been productive of important consequences in its extension to a number of other animals in which such an aperture was not previously suspected to exist. Müller brought this observation before the Berlin Academy, and it was noticed in the printed report of the proceedings in 1851. A more detailed account of his observations on this subject is given by Müller in his Archiv. for 1854 (p. 60.). The very thick covering of the ovum of Holothuria presents an appearance of radiated lines running through it perpendicularly to the surface, which resembles in some degree the marking in the membrane of the Fish's ovum, but is not so distinct, and does not appear, as in it, to be produced by visible tubes or pores passing through the membrane. The canal of the micropyle pierces the whole thickness of the radiated membrane; but Müller conceived that it did not perforate the delicate vitelline membrane placed on its inner surface. Leydig, however, and Leuckart are of opinion that the canal passes completely into the interior of all the egg-coverings, and reaches the surface of the yolk, so that it may convey the spermatozoa to that body. The entrance of the spermatozoa has not, however, as yet been actually observed.

According to Leydig, the thick membrane may consist of several layers united together, such as, internally the vitelline membrane, the thick albuminous part in the middle, and externally the nucleated layer formed by the remains of the ovarian capsule. Leuckart and Leydig have also pointed out the fact that the formation of the canal of the micropyle in the egg of Holothuria proceeds from or is connected with the original attached and pedicu-

* See Kölliker in Müller's Archiv. for 1843, p. 92; Tafl. vii., fig. 44.

† Details as to the structure of these ova will be found in the work of Von Siebold in Burdach's Physiologie, vol. ii.; in Dujardin's Hist. Nat. des Helminthes, see pl. ix. and xii.; in Blanchard's memoirs in the Annal. des Scien. Nat. for 1848, p. 321; in Van Beneden's work; and in Kuchenmeister's more recent Handbuch der Parasiten des Menschen, &c., Leipzig, 1855.

‡ Annal. des Scien. Nat., 1842, xvii.

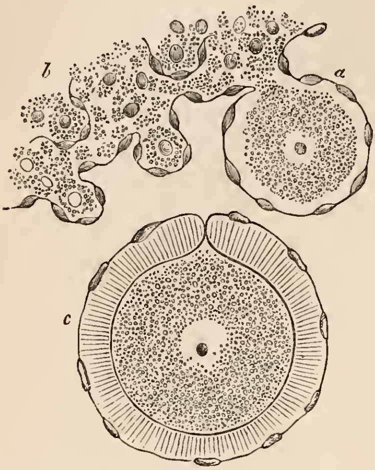
* Derbès, in Annal. des Scien. Nat. 1847, 3e Sér. vol. viii., p. 80, and Leydig in Müller's Archiv. for 1854, p. 312.

† Wiegmann's Archiv. 1844, and Annal. des Scien. Nat, 3e sér., vol. ii. p. 190.

‡ Leuckart in Bischoff's Wiederlegung, &c., 1854, and Leydig, loc. cit.

lated condition of the ovum in the ovary, that it is in fact the remains of the divided pedicle after the ovum is separated from the place of its original formation.

Fig. 91*.



Ovum and Micropyle in Holothuria tubulosa. (*From Leydig.*)

a, b. A small portion of the ovary from the inner surface, containing ova in various earlier stages of their development; three of them project from the inner surface, of which *a* is the most developed. In this one the pediculated attachment and enclosure of the ovum by the nucleated ovarian membrane is seen, the yolk granules and the germinal vesicle with its macula.

c. A more advanced ovum now separated from the ovary. Externally the nucleated remains of the ovicapsule are represented; inside this the thick albuminous layer marked with radiated lines, and lined closely by the vitelline membrane; both these, as well as the ovicapsule, being perforated by the micropyle formed at the place where the pedicle formerly existed.

The micropyle aperture has also been observed in other Echinodermata, viz. by J. Müller in Ophiothrix fragilis, in which he states its diameter to be $\frac{1}{1200}''$, and by his son Max Müller in Sternaspis thalassemoides.* This aperture has not yet been observed in the ovum of Echinus. In the fecundated ova of this genus, however, Derbès observed spermatozoa to have passed through the thick external albuminous covering, but not within the more delicate vitelline membrane; but in this animal the external covering is more like a layer of soft albumen than a dense membrane as in Holothuria.

The ova of Echinodermata take their origin, like those of other animals, by the formation of the germinal vesicles. These have been observed by Leuckart in the Holothuria tubulosa, beginning to be formed in the ovarian substance, which they cause to bulge or project when they enlarge, so as to hang into the ovarian cavity. The yolk-granules then come to be deposited round the vesicles, rendering the ova opaque, but during all this time the ovum is attached and enveloped by the original capsule derived from the ovary; the albuminous layer is then deposited, and the ovum being detached, the micropyle remains, as already stated, as the perforation in the pedicle of attachment.*

Polypina. — Although the greater number of the Polypi are commonly multiplied by a process of gemmation, as has already been stated in a former part of this article, yet they are all capable of attaining sexual completeness, and are also reproduced by means of fecundated ova. From the varieties, however, presented by the form both of the gemmules and true ova in different genera of Polypes, considerable difficulty has been experienced in determining the exact circumstances in which the ova are produced, and the distinction between the germs from which true ova and those from which gemmæ are formed. This is more especially the case among the ciliobrachiate Polypes or Bryozoa, which in their general organisation approach very nearly the tunicate Mollusca, but which in their mode of reproduction resemble closely some of the Polypes.

The ova of the common Hydra, already referred to in a previous part of this article, present the character common to the class, of being enveloped by a firm covering or shell membrane, which seems to be formed from modified cells, and which is sometimes beset with rough processes or projecting bristles or barbed spines somewhat like those of the Bryozoa.

In the Tubularidæ and Sertularidæ the ova are formed in ovigerous capsules, which may be regarded as modified individuals or polype-heads of the compound animal formed by gemmation. In some instances these are detached from the parent stem, as in Tubularia indivisa†; in other genera they remain attached, and their ova, or the ciliated embryos developed from them, are discharged from the cavities in which they are formed‡; but as the phenomena of the production of these ova have been fully described by Professor Rymer Jones in the article Polypifera, it is unnecessary to enter into farther details with regard to the process in this place.

* The micropyle was represented in the ovum of Holothuria tubulosa by R. Wagner in his Icones Zootomicæ, tab. xxxii., fig. 12., before its nature was known. The first discovery of a micropyle in the animal ovum is therefore due to J. Müller. The next observations of a similar nature are those of Leuckart and Keber.

* In addition to the memoirs previously quoted, descriptions of the ova of Echinodermata will be found in the following: viz., those of Comatula by J. Müller, in Mem. of the Berlin Academy for 1841; of Asteracanthion, in Wagner's Prodromus, and in the 5th Part of Carus and Otto's Tabulæ Anat. Compar.; those of Echinus by Derbès, loc. cit.; and by Krohn in Beitr. zur Entwick. der Seeigellarven, Heidelberg, 1849, &c.

† Sir John Dalzell, Remarkable Animals of Scotland, &c.

‡ Dumortier and Van Beneden's Researches, in Mem. of the Acad. of Belgium, 1842, tom. xvi.

In Hydractinia rosea, Van Beneden ascertained the existence of the germinal vesicle and nucleus within the ova while still contained in the capsule; and it appears that in all true ova of the Hydrozoa the vitellus, which consists of finely granular substance, undergoes a complete segmentation in the same manner as in other animals in which it presents a similar structure.

In the common fresh-water polype, in which ovigerous capsules, or ova, and spermatic capsules were found coexistent on the same individuals, I observed sometimes the spermatic capsules brought into contact with the surface of the ova by the bending round of the body of the polype at the time when the spermatozoa were being discharged. This took place previous to the formation of the firm external covering; but I could not determine whether fecundation had thus taken place or whether any spermatozoa had penetrated the ovum.

In some of the Hydrozoa, as in the common green polype, the ova are single, while in others as in Hydra fusca, figured by R. Wagner*, there are several ova enclosed in the same capsule.

It is remarkable that, while in some Hydrozoa the ova are developed from animals which retain the polype form in their complete sexual condition, or from modified polype heads, in others, as in Coryne, Fritillaria and Campanularia dichotoma, it is only from a medusoid progeny separated from the polype stock that the true fecundated ova are produced.

In Anthozoa, the most of which, as Actinia, Alcyonium, Veretillum, Gorgonia, and the Corallines are hermaphrodite, the ova consist of finely granular yolk, germinal vesicle and macula, and undergo complete segmentation.

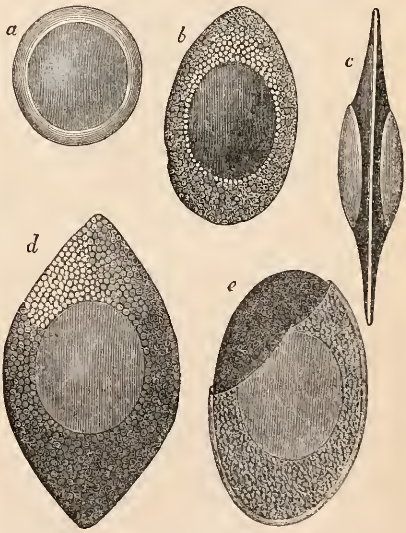
The Bryozoa may be most appropriately considered in this place, as they present considerable analogy to the compound polypes in the mode of their reproduction. They are of separate sexes, and appear to be propagated in three modes, viz.: 1st, by gemmation; 2nd, by true fecundated ova; and 3rdly, by bodies which have long been regarded as ova, but which according to Professor Allman's recent researches may rather be considered as peculiar encysted gemmules, and may probably be analogous to the so-called winter ova of Daphnia and Lacinularia to which reference has previously been made.

The development of the true ova of Pedicellina observed by Van Beneden has been already described.† In this instance the ova are arranged in clusters surrounded by a transparent capsule. In each ovum the finely granular yolk undergoes a complete segmentation. The germinal vesicle possesses a single macula.

According to Van Beneden and Dumortier‡, the ova of Alcyonella are developed in ovarian sacs connected with the inner end of the stomach. They are described as commencing by the formation of germinal vesicles with nuclei or maculæ, and as having subsequently the granular yolk-substance deposited round each vesicle; and these authors describe the same ova as acquiring at a later period the peculiar horny or cellular covering which forms the two-valved shell membrane long known as belonging to the winter ova of this and several other genera of freshwater polypes. But with regard to the nature of these bodies and the mode of their formation some doubts may arise in consequence of the researches of Professor Allman. The bodies in question are at first nearly spherical and of a light or milky colour; they become later of an oval form, and flattened or discoid, and the cells of the shell-covering are then developed, and acquire the deep brown colour which very generally prevails among these bodies when arrived at maturity, and which makes it impossible to trace farther the changes within the ovum. These cells are developed to a greater extent round the widest margin of the disc, so as to form there a thick ring or border, which is afterwards cleft in two when the valves of the shell open to allow the escape of the embryo.

The same authors have described the propagation of the Paludicella to take place in summer by means of buds, and in winter by

Fig. 92*.



Formation and Structure of the ova of Lophopus Bakeri. (*From Van Beneden.*)

These represent, according to Professor Allman, not the true ova, but the Winter ova or "Statoblasts." *a.* The ovum previous to the deposit of the cellular covering and marginal plate. *b.* This covering now in progress of formation. *c.* and *d.* profile and front view of the ovum, when completed, showing the structure of the cellular border which is afterwards cleft in two at the edge, when the embryo is about to escape.

e. An ovum at an earlier stage showing the ovicapsule in part removed from one side of the ovum and its cellular covering.

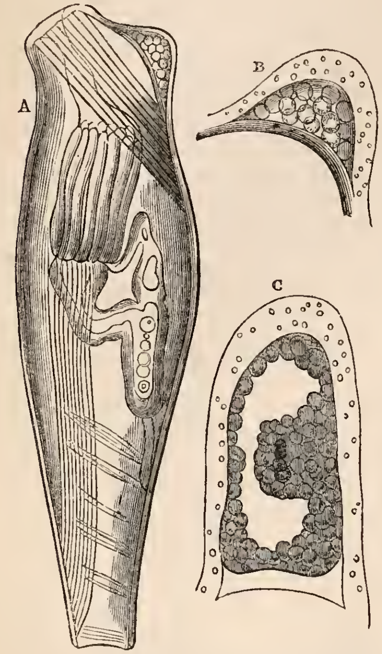
* Icones Zootomicæ.

† See p. 23. and *fig.* 19. of this article.

‡ Mém. sur les Polypes d'Eau douce. Acad. de Belgique, 1842.

means of true ova, as well as by attached buds, which last are then covered by a strong corneous envelope, and have received the name of propagula. In Fredericella they describe a propagation by means of buds and by ova provided with the strong horny envelope. In Alcyonella and Lophopus, besides the usual propagation by buds, and by the common ova, these authors have stated that there is also a viviparous production of ciliated embryos from ova which remain within the parent animals; but they have not stated particularly the manner in which these ova originate, nor their difference from those which receive the corneous envelope. The difficulties presented by these varieties seem to be in some measure removed by the view offered by Professor Allman of the nature of the bodies last mentioned, to which I will now advert.

Fig. 93*.



Formation of buds in Paludicella. (From Van Beneden and Dumortier.)

a. One of the Polypes of Paludicella Ehrenbergii contracted within its cell, showing at the upper part towards the right the commencement of the formation of the bud by the growth of cells between the outer and inner layers of the cell-wall.

b. The same bud a little more advanced and more highly magnified, represented by itself. The vesicular cells which separate the ectocyst and endocyst are seen more distinctly.

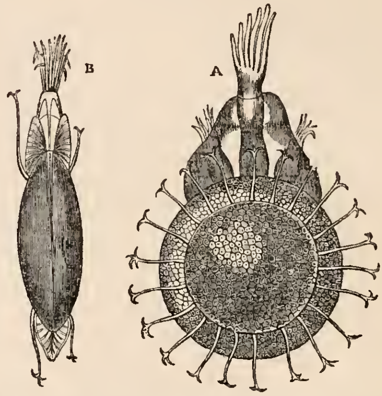
c. A more advanced stage of the same, internally; the part from which the embryo polyped arises is seen bulging out from the rest.

This figure has been introduced to show the difference between the process by which a true bud arises and that by which ova are produced.

It has long been known that the so-called winter ova, or the bodies provided with the corneous envelope, are formed chiefly towards the autumn and winter season; and the strength of their covering has generally been regarded as a provision for the protection of the germ from the hurtful influences of the winter season. During two seasons I have observed the production of these bodies from the Plumatella repens; and I have kept them through the winter till the polypes were developed, and issued from them in the ensuing summer.

From his careful observation of these bodies in several genera, Professor Allman has arrived at the conclusion that they are not, as was previously supposed, true ova, but rather separated gemmules; and he conceives that Van Beneden, who has described their form and structure so well, must have confounded them with some other bodies in their first or earlier stages, or has failed to distinguish between them and the true ova. This distinction Allman has succeeded in making by ascertaining that the true ova and these bodies do not arise in the same situation, and that these winter ova or gemmules do not in their earliest stages present any germinal vesicle or macula as the true ova do, and do not afterwards undergo any segmentation. They are formed, according to Allman, in the funiculus which connects the bottom of the stomach with the inside of the cell of the polypide, the same body which was described by Van Beneden and Dumortier as an ovary, but which Allman regards rather as analogous to the gemmiferous stolon of the solitary Salpæ. These bodies Professor Allman proposes to call stato-blasts. He farther discovered that there is a true ovary with genuine ova which may be distinctly observed in Alcyonella, and which is situated in the walls of the endocyst

Fig. 94*.



Winter ovum and embryo of Lophopus Crystallinus. (From Van Beneden and Dumortier.)

This is the same as that represented by Turpin under the name of "Cristatella mucedo." In A. the flat surface, and in B, the narrow edge of the ovum, is represented. The two valves of the egg covering have opened superiorly, and the embryo, which already possesses three crowns of tentacles, is seen escaping.

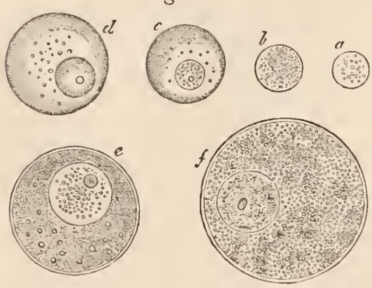
near the anterior extremity of the cell. A number of ova were found in the ovary containing the distinct germinal vesicle with macula. He also observed the segmentation of these ova in the usual manner, and the conversion of the segmented mass into a ciliated embryo, within which the new polype is subsequently developed.†

Should these observations prove correct and be applicable to the other instances of similar winter ova among the Bryozoa, they may tend to remove some of the difficulties which exist in regard to the various reproductive bodies occurring in these animals; but farther researches seem still necessary to point out in these and in other polypine animals more fully and minutely the relation between the three kinds of reproductive bodies, viz., true ova, separated gemmules, and attached buds.

Acalephæ.—It is remarkable that notwithstanding the very close relation in which these animals stand to the Anthozoid Polypes, the form of their ova is not the same. The Discophora (Medusæ) are of distinct sexes: the Ctenophora (Beroes) are hermaphrodite; the Siphonophora (Diphyidæ) are various, or bear, in the manner of compound animal stocks, a variety of zoids, sometimes of one sex alone, at other times of different sexes on the same stem.

The structure of the ova in Medusæ is extremely simple. They are originally formed from minute cytoblasts which soon acquire a single nucleus or macula, and are enclosed in a delicate external membrane. These constitute the germinal vesicles, round which the granular yolk-substance is gradually deposited in increasing quantity. The complete segmentation of the yolk has been observed by Von Siebold in Cyanea aurita.* The yolk-substance is often highly coloured, violet or yellow. In the former part of this article I have referred to the manner in which some compound Hydroida are propagated through their medusoid progeny. These medusoid individuals, like the ordinary Medusæ, are of separate sex; and they must therefore be looked upon as the complete stage of the polypine animals from which they have proceeded, whether they have their young developed while the parent remains attached to the nursing polype stock, or have assumed the separate and independent mode of life in a more complete state of development. There are many varieties in the degree of perfection to which they attain even while remaining attached to the polype; but the general principle of formation is the same throughout the whole of the hydroid animals, the remarkable and constant fact with regard to the mode of their reproduction being this, that the immediate product of development from the ovum which has been formed by sexual generation from a Medusa or medusoid animal is invariably an attached Polype, and that the medusa or medusoid is the product of a non-sexual process of gemmation from this polype stem.

Fig. 95*.



Development of the ova of Acalepha.

These figures give magnified views of the different stages of formation of the ova taken from the ovary of a large Rhizostoma. *a.* The primitive germ. *b.* The germinal vesicle now present in the primitive ovum. *c. d.* The same more advanced and enlarged, the macula has appeared in the germinal vesicle, and a few yolk granules are deposited in the clear vitelline substance. *e.* The yolk granules greatly increased in quantity and becoming opaque, a vitelline membrane is now formed. *f.* The same somewhat more advanced, the yolk granules are now collecting together to form corpuscles. The macula is assuming the elongated form.

Protozoa.—With regard to the Protozoa, or Infusoria and Rhizopoda, it is unnecessary to add anything here to what has been stated in the several articles on these subjects and in a former part of this one, excepting the remark, that continued researches appear to show that as the sexual distinction has not been detected, and may probably be absent in these animals, the nucleus of the monocellular forms of these beings may hold the place of the germinal vesicle in them, and that the processes of division and production of internal gemmules takes the place of true ovulation. At the same time it must be admitted that it is by no means improbable that the sexual relations may yet be discovered in the lowest monocellular animal bodies, as has recently been the case in some of the simpler and monocellular Algæ, and that as our knowledge of the process of reproduction in these beings is still very limited, it may be destined to undergo even greater progressive changes than those which it has suffered from the researches of the last few years.†

Porifera.—The bodies which have usually been regarded as the ova of Sponges, and to which a reference was made in the earlier part of this article, are of two kinds, viz. gemmules or detached ciliated portions of the

† Proceedings of British Association for 1855. See also Professor Allman's interesting Report on the Polyzoa to the British Association. See Trans. for 1850, p. 320.

* Beitr. zur Naturgesch. der Wirbellos. Thiere, 1839.

† See the papers of Focke, Cohn, and Stein referred to in the first part of this article, and the more recent work of Stein, "Die Infusionsthiere auf ihre Entwickelungsgeschichte untersucht." 4to. Leipzig, 1854.

substance of the sponge, and certain spherical bodies enclosed by dense capsules, which are produced towards winter, and which appear to contain a number of germs, each of which is capable of being developed into a Protean animalcule, from which probably a sponge may proceed.* But it may be doubted whether these last-mentioned capsules are true ova or may not rather be of the nature of the gemmules, winter ova, or statoblasts of Professor Allman; and it is important to notice that Mr. Huxley has recently discovered in Tethya a different set of bodies, which contain all the essential parts of true ova, viz. vitelline membrane, yolk, germinal vesicle, and macula, and that these bodies, which are situated between the cortical and central substance, are imbedded in a mass of cells together with spermatozoa.† Although the individual living particles of the sponge closely resemble simple ciliated infusoria, and the mass may, therefore, be viewed as an aggregate of these minute beings, yet its analogies with and transitions towards the fungiform polypes are so great, that we may expect ere long that the phenomena of its reproduction may be placed in a new and clearer aspect by the continuation of the researches now noticed, and by others of a similar kind.

RECAPITULATION AND CONCLUSION.

Having now stated in detail the principal facts that have come under our knowledge with regard to the form, structure, and mode of origin of the ova of different animals, it may be proper, in bringing this article to a close, to endeavour shortly to deduce from these facts the most general results to which they appear to lead. These results, together with some reflections on our subject, may be stated under the following heads, viz. 1. Definition of the ovum, as related to its own structure, and its history in connection with the reproduction of the species. 2. Recapitulation of the most general facts ascertained by the comparison of the ova of different animals. 3. Morphology of the ovum; homology of its parts; and relation of the ovum to other organic structures. 4. Phenomena attendant on the maturation of the ovum. 5. Relation of the ovum to fecundation by the male sperm. 6. Immediate effects of fecundation on the ovum; and relation of the ovum after fecundation to the first commencement of the process of embryonic development.

1. Definition of the ovum, as related to its own structure, and its history in connection with the reproduction of the species.

In the commencement of this article the ovum was shortly defined as "the product of parental sexual generation from which the young of animals are developed (produced)." This definition appears correct and sufficiently comprehensive; but should it appear desirable to substitute for it a more precise description of the characteristics of the animal ovum, the following may be proposed as applicable to the ovum throughout the whole animal kingdom, without involving any merely theoretical view of its structure and constitution, viz. "the ovum may be shortly described as a detached spheroidal mass of organised substance, of variable size, enclosed by a vesicular membrane, and containing in the earlier periods of its existence an internal cell or nucleus; these parts, formed by the female individual or organ of animals, are capable, when fecundated by the male sperm of the same species, of giving rise, by the series of histogenetic and organogenetic changes known under the general term of development, to an embryo, from which either directly or mediately the individuals of the animal species to which the parents belong are reproduced."

We thus separate from the category of true ova all those bodies of an apparently reproductive kind which are not the direct product of an act of sexual generation. To such bodies, the nature of which is as yet doubtful, and probably somewhat various, the indefinite appellations of buds, bud-germs, gemmæ, spores, winter ova, ephippial ova, statoblasts, &c., have been given according to the circumstances in which they are severally produced.

In all animals, then, with the exception of the Polygastric Infusoria and Rhizopoda, the occurrence of sexual generation and the formation of true ova are proved to be the regular and constant means for the permanent reproduction or maintenance of the species. In the exceptional instances now mentioned, and even in some others possessed of the sexual distinction, the best known and most common multiplication of individuals takes place by a subdivision of the parent body, either by fissiparous cleaving or by gemmation; but in them also it can scarcely be doubted that there are other means by which the permanence of the species is maintained.

All the most accurate recent investigations lead to the conclusion that the production of the young of all organised beings, even the simplest of the Protozoa, does only occur by direct connection through some organised medium with other beings of a similar kind or species. We are forced, therefore, to conclude that in the propagation or production of these simple beings, in circumstances where their more ordinary fissiparous or gemmiparous mode of multiplication cannot be admitted to have taken place, there must have passed from the bodies of the progenitors minute particles of organised substance (capable, as we know, of being suspended in the atmosphere, and of resisting during a long period many of those influences which generally prove inimical to animal development), which particles, when brought into circumstances favourable to the progress of the vital processes, undergo the cycle of changes necessary for the reproduction of beings similar to those from which they sprang. If there is any constant law which seems more certainly

* See Carter in Annals of Nat. Hist. vol. iv. p. 89.

† See Mr. Huxley's paper in Annals of Nat. Hist., 2nd series, vol. vii. p. 370.

than others to result from all recent researches into the history of organic nature, it is this necessary connection by descent of one being or set of beings from another.

In all animals, with the exception of the simplest tribes already referred to, the descent from parent to offspring is through a product formed and perfected only by the concurrence of male and female organs; but we are still at a loss to determine whether the unseen germinal bodies by which the Protozoa are reproduced are of the same or of a different nature. The structure of some of these germinal bodies as described in the earlier part of this article (p. 7., &c.), bears a very great resemblance to that of true ova; but yet the sexual distinction of the parent animals has not yet been discovered. The recent researches of naturalists indeed show that our whole knowledge of the history of the Protozoa may be considered as only in its infancy. The discoveries as to the encysted stage of existence among the Vorticellæ and Gregarinæ and others, the phenomena of conjugation observed in Gregarina and Actinophrys, the entire knowledge lately gained of the form, structure, and habits of the Foraminifera, all point to important future discoveries and modifications of our hitherto crude and imperfect views of these tribes of beings, and must make us refrain from attempting at present to form any opinion or even conjecture as to the modes of their reproduction; while at the same time the recent discoveries as to the existence of the sexual distinction in the simplest forms of plants encourage the hope that ere long the reproduction of the Protozoa may, in a similar manner, be removed from the obscurity in which it now lies hidden. It does not appear necessary from these considerations that our definition should make any direct reference to animal bodies of the nature of which our knowledge is still so imperfect.

The result of development from a fecundated ovum in all vertebrate and in a considerable number of invertebrate animals, is the formation of an embryo which, by a process of progressive growth, arrives at maturity, and assumes the form, structure, and habits, either, as the case may be, of a hermaphrodite animal, or of the parent of either sex. In a certain number of these instances, as in Batrachia, Insects, Crustacea, and others, growth is not altogether continuously progressive, but is subject to one or more breaks or changes as it were, which are marked by some change in the mode of life, or some difference in structure of the individual. To such marked changes in the course of the development or growth of an individual animal proceeding from a fecundated ovum, the name of Metamorphosis is given.

But from the facts narrated in the earlier part of this article, it appears that in a certain number of the invertebrate animals, such as those which have been referred to under the heads of Echinodermata, Polypina, Acalepha, Tunicate Mollusca, Trematode and Cestoid Entozoa, Annelida and Insecta, a very different result may, either regularly and constantly in some, or only occasionally in others, attend the first development from the fecundated ovum. To this modification of the developing and reproductive process the appellations of Alternate Generation or Metagenesis have been given, of which terms the latter may perhaps be the most appropriate. The phenomena which have been described under this head are so very various, that it is difficult, if not impossible, to give a short and general statement of their nature. The difference between this and the better known form of direct generation may, however, be stated nearly as follows:—In the Metagenetic form of reproduction the individual formed by the development of the fecundated ovum is generally different in aspect, structure, and mode of life from the parent or parents by which the ova were produced; this individual, or zoïd, though possessed, in many instances, of an organisation and of powers which fit it for the efficient performance of many of the most important acts of independent animal existence, is yet wanting in the attribute of perfect animal maturity, viz., the sexual organs and activity, and is consequently incapable by itself of an act of true generation, or, in other words, of the formation of fecundated ova, by which alone the species can be permanently reproduced. In such instances, then, it is only by the formation from these intermediate beings of others which are sexually perfect, that the generative act can be repeated. There are two phenomena requiring to be distinguished in connection with the most common forms of this process; the one the frequent multiplication of the imperfect intermediate beings, or zoïds; and the other the production either directly or by a succession of acts of development from the intermediate beings of those which are sexually perfect, or which resume the form belonging to the parents from which the fecundated ova were derived. It seems proper, therefore, to distinguish between an act of true sexual generation, and that by which new beings are formed from the intermediate individuals (or so-called nurses of Steenstrup, or zoïds of other authors); the first consisting invariably in development from a fecundated ovum; the second being probably more analogous to a process of budding or gemmation from a parent stock. It must be confessed, however, that we have still much to learn regarding the phenomena of this process, before we can form any general notion of its nature. The whole subject is replete with the deepest interest not only in connection with the history of reproduction, but in its influence, as stated in some parts of the preceding article, on the whole range of zoological classification and distinction. Our extended definition comprehends an allusion to these phenomena.

Lastly, the ovum may be considered as having two phases or stages of existence; the one in connection only with the female parent or female organ, in which the greater part of the organised material first to be employed in development is provided, and in which the ovum arrives at a certain stage of maturity; and the other in its relation to fecundation, or to the influence of the product of the male by which its developing powers are awakened or called forth. The mature ovarian ovum may therefore, in one sense, be looked upon as complete, if we regard only its own structure; but here its progress would be arrested without the occurrence of fecundation, and if we view it, therefore, with reference to its more important destination as the means of continuing the animal species, the ovum can only be regarded as perfect when that hitherto inscrutable change has been effected on its substance by admixture with the minute elements of the sperm in fecundation. The constancy of this law in the whole animal kingdom, with the exception of those of the Protozoa already referred to, makes it proper that our definition should make reference to fecundation as the means of perfecting the ovum. To the nature of this process itself a further allusion will hereafter be made.

2. Recapitulation of the most general facts ascertained by the comparison of the ova of different animals.

The ova of animals in their complete state may be considered as consisting of two sets of parts which are of very different relative importance in connection with the development of the embryo: the first of these sets of parts belong to the ovarian ovum, and are formed previous to their quitting that organ; the others are subsequently formed, and may be looked upon as accessory. These last often present great varieties, so as to cause the external form and appearance of the ova of animals to differ widely, while the ovarian part much more nearly corresponds. To this ovarium ovum we shall principally confine our present remarks.

An extended comparison of the ovarian ova of animals belonging to almost every family of the animal kingdom has shown that, notwithstanding great differences in size, and some variation in form and structure, they all agree in consisting of three essential and nearly similar parts before the period of their detachment from the ovary: these are, 1st, The internal nucleated cell or germinal vesicle with its macula or maculæ; 2nd, The vitellus, or yolk-substance; and 3rd, The enclosing vesicular envelope, or vitelline membrane. In all animals there is, also, a general similarity in the manner in which these parts are formed and combined so as to constitute the ovarian ovum; the germinal vesicle is the first produced, and may be regarded as the ovigerm; the yolk-substance next gradually envelopes it or is deposited round the germinal vesicle, and in general the vitelline membrane which encloses the whole is the latest formed.

The most marked differences among the ova of animals are connected with the structure of the yolk and the relation which it bears to the formation of the germinal part out of which the embryo is afterwards developed. Founding upon this difference, three groups, two principal and one subordinate, may be distinguished among the ova of animals:— 1st, The group of small-yolked ova, to which belong those of Mammalia and a considerable number of invertebrate animals, such as most Mollusca, the lower Crustacea, most Annelida, the Entozoa, Rotifera, Echinodermata, Acalepha, and Polypina. In this group, the ovum is generally of small or of moderate size, as a whole; the vitelline substance consists entirely or chiefly of fluid with fine granular particles, and the entire yolk undergoes segmentation: the entire yolk mass, therefore, is directly *formative*, or is employed from the first in the formation of the blastoderm or organised substratum in which the embryo is developed: the germinal vesicle is in this group usually of small size, and has only a single macula, or one composed of very few particles.

The second principal group comprehends the large-yolked ova, such as those of Birds, Scaly Reptiles, Cartilaginous Fishes, and the Cephalopoda, to which, perhaps, may be added Insects, Arachnida, and most Crustacea. In this group, the largely developed yolk contains, suspended in its basement, homogeneous substance, two kinds of organised corpuscles, viz., 1st, A certain portion of the small granular part, similar to that of the small yolked ova, which occupies a limited but determinate place in the ovum, and in its centre the germinal vesicle is situated; and 2nd, A larger portion of spherules, cell-like or other corpuscles of greater magnitude. It is the first or finely granular portion only which is immediately germinal, or which is subject to segmentation and forms the basis of the blastoderm; the remainder, or large cellular portion, is only secondarily employed in supplying nourishment to the embryo or its accompanying organised parts in the progress of their development. In the ova of this group, therefore, we distinguish the formative or directly germinal portion of the yolk-substance from the indirectly *nutritive* portion. In these ova, the germinal vesicle is also proportionally large, and the contents of the vesicle, though consisting in the earliest stages of their formation of a single macula, or of a very small number, very soon become converted into very numerous maculæ, or into a fine granular pulp.

The third, or subordinate group, may comprehend the ova of Amphibia, or scaleless reptiles, and osseous fishes, to which, perhaps, may be added some of the invertebrate animals mentioned under the second group. The ova of this group are intermediate in their structure between those of the first and second: they have certainly the greatest affinity with the large-yolked group, but there are many gradations among the ova of this kind, among allied species of animals, and it is chiefly on the ground of the incompleteness of the segmentation that I have thought it proper to arrange them in a separate group.

It may be remarked further, that in all animals, whatever may be the ultimate structure of the yolk, the primitive yolk, or that which is first formed, is invariably of the finely granular kind, — the cellular or large corpuscular yolk-substance is of later formation. These two parts remain distinct from each other, and the finely granular or formative yolk is that in which the germinal vesicle is invariably imbedded. In those instances, such as the Bird, Reptile, &c., in which the large cellular yolk greatly preponderates over the formative yolk-substance, the latter assumes in the later stages of formation the shape of a flattish disc on one side of the greater mass of the yolk, with the germinal vesicle placed in its centre.

The vitelline membrane presents some varieties in structure, being in some animals very delicate and homogeneous; in others, as Mammalia, remarkably thick, tough, and elastic, but without visible structure ; in a third set, exhibiting peculiar structure, such as the finely tubular perforations of the external membrane of the fishes' ovum, or the radiated markings in the ova of Holothuria or Cestoidea ; but in these last three instances the vitelline membrane is probably associated with additional layers of substance derived from a different source from that which forms the homogeneous membrane.

A remarkable peculiarity has recently been discovered in the enclosing membrane of the ovarian ovum of some animals, in the aperture or micropyle which has been observed in osseous fishes, insects, some Crustacea*, the Acephalous Mollusca, some Annelida, Holothuria, and some other Echinodermata. There seems reason to believe that a similar aperture exists in the ovum of Batrachia and Cephalopoda; and it is very probable that it may yet be discovered in other animals. At the same time it is right to state that in Mammalia and several other animals it has been most carefully sought for without success. This aperture appears to be designed to admit the spermatozoa into the cavity of the ovum, or into contact with the yolk-substance and germ, in those instances especially in which the egg coverings are thick and tough, and fecundation is late of occurring.

The relation of the ova to the ovaries or organs in which they are produced, exhibits considerable varieties in different animals. 1. The most common is that in which the germs of the ova arise within minute close follicles or vesicles, which are imbedded in the more or less solid or loose stroma of the ovary ; the follicle enlarging with the ovum as its other parts are added till the period of of maturity, when, periodically, the follicles open for the escape of the ova. 2. In a second form, as in Nematoid Worms and Insects, the germs of the ova are produced free in the upper part of an ovarian tube, and the yolk-substance, &c. are added gradually as the egg germs descend through successive portions of the tube : here no true dehiscence is necessary to allow of the escape of the ova. 3. In a third form, as in Trematode and Cestoid Entozoa, distinct organs are provided for the formation of the ovigerms and the yolk-substance, and these last are brought together and combined into the spherical form of an ovum in another part of the genital apparatus. 4. In the greater number of animals the germs for each ovum appear to arise singly, and the ova are thus isolated from the first ; but it would appear that in some animals these germs arise in groups, perhaps by development from a common germ, so that they are from the earliest period connected together by pedicles. Yet, with all these differences, there is to be perceived, on the whole, a general similarity in the plan of formation of the parts of the ovum itself in different animals. This plan may be generally stated as follows.

The germinal vesicle is universally the first part of the ovum which makes its appearance ; it does not appear to be nucleated or to possess its macula from the first in all instances, and this macula cannot therefore be regarded as the centre of its formation. The germinal vesicle is generally at first only a minute point ; it soon enlarges, however, and either possesses from the first, or at a very early period acquires, its macula or nucleus. In animals with the solid follicular ovary, each follicle is occupied by a single ovum, which begins within it as a minute germinal vesicle. The delicate wall of the follicle is also perceptible at the same time as the ovigerm ; indeed, there is reason to believe that it even precedes the commencement of the formation of the ovum, though this is a point not yet fully determined. In those animals, on the other hand, in which the ovary is tubular, the ovigerms appear, in some instances at least, to arise in groups within cells; and it may be a question whether these cells bear to the ovigerms arising within them the relation of the ovarian follicles of solid or closed ovaries. Whether this be so or not, that relation is in most instances speedily changed, as the ova soon become free, or, in others, are attached by a pedicle to a common stalk.

The wall of the ovarian follicle consists at first of an extremely delicate vesicular membrane, which is the same as that to which the name of ovicapsule or ovisac has been given. At a very early period, and while the ovum consists of no more than the germinal vesicle, the homogeneous wall of the follicle is lined with a layer of flat cells somewhat analogous to some forms of epithelium : this is the commencement of the structure which in Mammalia afterwards forms the tunica granulosa, and the fluid and cellular contents of the Graafian follicle. It appears to have various destinations in different animals.

The second stage in the formation of the ovum is the deposit of the vitelline substance around the germinal vesicle. In most animals the yolk-substance, when it first begins

* It has been inadvertently stated in a preceding part of this article (p. 116.) that the micropyle had not been observed in the ova of Crustacea, whereas Meissner has ascertained its presence in that of Gammarus. (See his Memoir in Zeitsch. fur Wissen. Zool. vol. v. p. 284.)

to be formed, is scarcely granular, and in some instances quite clear, consisting of a viscous blastema, and as it increases separating the germinal vesicle within from the ovarian follicle, which expands proportionally. Very soon, however, and in many animals indeed from the first, fine opaque granules make their appearance, as if by precipitation or deposit, in the clearer basement substance, and thus the primitive yolk-substance of the ovum in all animals is formed. In most instances there is a time during which the ovum, consisting of germinal vesicle, with a small quantity of primitive yolk, exists, without any other covering than that given to it by the ovarian follicle; but as the deposit of the finely granular yolk increases, and at a very variable period in different animals, the vitelline membrane is formed round its exterior. The addition of this covering may be regarded as the third stage in the formation of the ovum. The manner of the origin of the vitelline membrane has not yet been accurately observed; and it is probable (as will be hereafter stated) that the coverings known under this name may have different modes of origin; but if we restrict our attention at present to such simple ova as those of Mammalia, I believe it may be stated as extremely probable that the so-called zona pellucida which constitutes the vitelline membrane of the Mammiferous ovum, takes its origin by the consodidation of the superficial part of the basement substance of the primitive yolk.

It appears probable that in the large-yolked ova, such as those of the bird, the vitelline membrane, which we find enclosing the whole mass of the yolk, owes its origin to a different source; and I am inclined to believe that in this and in many other animals the membrane which we term vitelline, as being the immediate investment of the yolk, is not of the same nature with the zona pellucida, or the simple homogeneous vesicle of the smaller ova, but rather a structure of later formation, which owes its origin to the fusion, or amalgamation, or to some other change in the outermost layer of cells which form the nutritive yolk of these animals.

In connection with this view, it is important to remark, that at that earlier stage of formation of the bird's egg when it consists entirely of formative or primitive yolk, there is an approach to the formation of a zona, in the existence of a very distinct, clear, and consistent marginal portion of the yolk blastema, from which the yolk granules seem to retire. When the large cellular or nutritive yolk is formed, this temporary zona seems to disappear, and to be replaced externally by the permanent vitelline membrane already mentioned.

In those animals in which the ovigerms arise by development within cells so as to be connected in groups (Gordiacei), and in some others, the vitelline membrane, or a substitute for it, seems to be formed from the earliest period in a different manner from that now described.

The germinal vesicle is unimacular in general in the small-yolked ova, and multimacular in the large-yolked ova, and also in the intermediate kinds. In the latter it is rare to observe the earliest stage in which the macula is still single: the multiplication of the maculæ takes place with remarkable rapidity, and apparently by a process of endogenous development, or possibly by division. The ultimate destination of these maculæ is still a subject of doubt.

3. Morphology of the ovum; homology of its parts, and relation of the ovum to other organic structures.

Should the views be correct which have now been stated with regard to the relations of the parts in the mature ovarian ovum, and the manner in which they are formed, it will be apparent that a strict homology or anatomical correspondence can be pointed out in regard only to some of the parts which are recognised under similar designations, as respectively belonging to the ova of different animals. All physiologists will probably be disposed to look upon the germinal vesicle or ovigerm as corresponding or homologous in the ova of all animals, and, notwithstanding the great differences known as to its more simple or multiple condition, the same view may also be taken of the structure known as nucleus or macula. The primitive or finely granular yolk-substance, more especially that which immediately surrounds the germinal vesicle, and is afterwards employed in the formation of the blastoderm or embryogerm, seems also to have a similar origin, structure, and relation in all animals. But beyond this it is more difficult to trace the homological correspondence; for under the names of cellular yolk-substance and vitelline membrane it appears that there have been brought together parts of which the origin, structure, and relations may be dissimilar in different animals. There seems at least to be sufficient reason, from what is already known of the varieties of the enclosing membrane, or so-called vitelline membrane, to establish a distinction between several forms of that structure; as, for example, between the vitelline membrane, which exists from the earliest period as a pediculated sac in connection with the ovarium, as in Holothuria; that which is derived from the extension of the wall of the original germ-cell in grouped ova, such as have been described by Meissner in Gordiacei; that which is later formed round the ovum of Mammalia as a zona pellucida, by the consolidation of the outer layer of the primitive basement substance of the yolk; and that which in the bird and other animals whose ova are similarly constituted, appears to derive its origin in part, at least, from coalesced cells corresponding to those of the tunica granulosa of the ovarian capsule on the exterior of the cellular yolk.

With regard to the cellular yolk itself, we must refrain from any attempt to establish its homology till we shall be more fully acquainted with the mode of its production; for it is still undetermined whether it arises by cell formation within the primitive vitelline membrane through some change in the substance of the primitive yolk, or whether it is derived, as I am inclined to believe may be the case in birds and some other animals, in a space external to these parts, and more in connection with the cellular contents of the ovarian follicle.

In limiting, then, our comparison to the parts of the ovum in a bird and a mammifer, we may regard the germinal vesicles as homologous in both; the finely granular germinal disc of the bird's ovarian egg as homologous with the whole vitellus of the mammiferous ovum; the zona pellucida of the mammiferous ovum as temporarily represented by the clear outer band of the primitive yolk, which is seen in the bird's ovarian ovum when of a diameter of from $\frac{1}{40}$ to $\frac{1}{20}$ of an inch; the cellular yolk of the bird's egg, and its enclosing vitelline membrane as probably homologous with the fluid and granular contents and lining tunica granulosa of the ovarian follicle of the mammifer, and not by any means with the corpus luteum of a later period, as has been suggested by some. The albumen of the bird's egg has its homologue perhaps in the similar deposit which the ova of several Mammalia acquire in their descent through the Fallopian tube. The chorion of the ovum of Mammalia, being an after growth, has probably no true homologue in the bird's egg, unless we should regard the shell membrane and shell as occupying this place.

Many ovologists have thought it of importance to establish a comparison between the ovum or its parts, and some one or other of those microscopic structures which, since the publication of the discoveries of Schleiden and Schwann, have been known as organised cells. Schwann himself, though looking upon the entire animal ovum as a cell, entertained some doubts as to the exact nature of the comparison to be instituted for its several parts. These doubts are not yet removed, and the progress of knowledge has tended rather to diminish than to increase the appropriateness of the comparison, more especially from the somewhat various and indefinite nature of the bodies which are now recognised as organised cells.

It cannot be denied that, if we regard merely the structure of the simpler ova of small animals, we find in them the general characteristics of an organised cell, as these have been usually understood; that is, we find the external structureless vesicular cell-wall, the internal granular contents, and the internal nucleus or inner cell with its nucleolus. But when we consider more fully the whole history even of the most simple ova, and extend our regard to the structure and history of the more complex forms of ova, we perceive many circumstances which render the comparison with detached animal cells inapplicable.

Leuckart remarks, in his article Zeugung, previously referred to (p. 815.), that if we attempt to deduce the most general result from what has been ascertained as to the formation of the ovum, it is this, that "the animal ovum is formed by deposit round the germinal vesicle." The progressive formation of the parts of the ovum, therefore, would appear to differ widely from that which Schwann held to occur in most cells. But our whole knowledge of the various forms and modes of production of cell-like structures has been extended, and has undergone some modification since the time of Schwann; and there are now known to be not a few cell structures which are formed by external deposit of matter round a nucleus, nearly in the same manner as occurs in the ovum. In this view, therefore, the simpler kinds of ova might be regarded as examples of "deposit cells."

The great variation in the magnitude of different ova, and the prodigious size which some of them attain, as compared with the minute and generally microscopic size of the organised cells of the animal body, cannot by itself be received as a conclusive argument against the cellular constitution of the ovum; but the complexity of its structure, its relation to fecundation, the peculiar micropyle of the outer wall in some, the separation of the germinal from the nutritive part of the yolk-substance, and the new formation of cells after segmentation in a limited or more extended space over the yolk in the interior of the vitelline membrane, are so widely different from any thing belonging to the history of other cells in the animal body, that we are forced to regard the ovum rather as a structure of a peculiar kind than as a mere modification of a cell.

The germinal vesicle it might be held, both in its structure and its mode of origin, merits, more justly than the whole ovum, the comparison with an organised cell. But even in its history there are points of difference, and we are still too little acquainted with the mode and consequences of its disappearance at the time of the maturation of the ovum, to warrant our making more than a vague and general comparison of the germinal vesicle to an organised cell. In admitting that the ovum, or its germinal vesicle, present some of the features of the organic cellular structure, we ought always to bear in mind that they are the source of all the other cells from which the animal body is developed.

The manner of the very first origin of the germ of the ovum is still involved in obscurity, for we only know of the existence of an ovigerm when the germinal vesicle has attained an appreciable size. Whence the first germs of the germinal vesicles proceed can as yet be matter only of conjecture. Without entering here upon the debated ground of the origin of organised cells in general *, I would venture to express the opinion, that as there is no ovigerm without a parent, so there is no new organisation without previously existing, and at some time or other connected, organisation. Hence, notwithstanding the appa-

* See upon this subject the very interesting and suggestive Review by Mr. Huxley in the Brit. and For. Med. Chir. Review for October, 1853.

rent isolation of the origin of cells in blastema or intercellular substance, it might still be held that the unseen germs of new cells contained in that blastema may have derived their origin from other cells or organised parts proceeding from cells. And thus, in regard to the first origin of the ova of animals, it is fair to conjecture that the germs from which they spring have taken their descent from parent cells or structures derived from cells through the organs appropriate to their formation. But here observation fails to assist us further, and we are lost in the region of speculation.

If, however, with the reservations now stated, it should be thought desirable to compare the ovum to the organic cellular structures, the germinal vesicle may be regarded as the simple cell of the ovum, the whole ovum as a complex cell; the first of these being formed probably by expansion from a minute point or molecule, the second by superposition or external deposit round the internal cell; but both at the same time presenting features which are peculiar to themselves, and different from those which characterise other cells of the animal economy. The different and separate formation of the germinal vesicle and yolk, which is perceptible to some extent in the ova of most animals, is placed in its most striking point of view by those instances in which, as in Trematode and Cestoid Entozoa, there are distinct germigenous and vitelligenous organs, and those in which, as in Nematoidea and Insecta, the ovary is tubular, and the formation of the several parts of the ovum goes on progressively in different parts of the tube.

4. Phenomena attendant on the maturation of the ovum, and its discharge from the ovary.

The ovum naturally undergoes in the ovary a progressive development till it arrives at the state of maturity, when it is usually separated from the ovary by a process of dehiscence, is conducted through the female passages either to be excluded or laid, as in oviparous animals, or to be retained in a uterus or other part of the female organs in viviparous animals during uterogestation. The maturation of the ova and their separation from the ovary is in many animals periodical and independent of fecundation. This natural periodical separation of the ova has been termed *Ovulation* by some authors.*

The change which the germinal vesicle undergoes at the period of the maturation of the ovum has naturally attracted much attention, from the hope that through the observation of this phenomenon some explanation might be obtained of the first origin of the germ round which, after fecundation has taken place, the segmenting and organising stratum is collected, from which the blastoderm is produced; but it must be allowed that as yet little success has attended our efforts to detect the connection, if it exists, between these two processes. In almost all animals the germinal vesicle is lost to view at the time of the maturation of the ovum, and generally before or about the time when the ovum leaves the ovary. In large-yolked ova the maculæ of the germinal vesicle become very numerous by their multiplication and sub-division at an early period; while in the small-yolked ova, as has been observed in a few animals at least, the increase in the number of the maculæ does not take place till immediately before the diffluence or disappearance of the vesicle. The more minute phenomena of this diffluence are as yet very imperfectly known. In some animals, as Mammalia and Birds, it has been observed that shortly before the diffluence of the vesicle, its delicate wall undergoes a softening or approaching solution, so as to make it impossible to separate the vesicle entire. After this, when the diffluence is complete, the contents disappear from the situation they have previously occupied, but what becomes of them has not yet been determined. In some instances, as Birds and Batrachia, it has been observed that, after the diffluence of the germinal vesicle, the germinal part of the yolk, which previously consisted exclusively of small opaque granules, is now mingled throughout with clear hyaline spherules, somewhat similar to the dispersed maculæ of the germinal vesicle; but it is only matter of conjecture that these clear spherules have been derived from the germinal vesicle or its maculæ.

In a few instances, as in Ascaris, it has been thought that the entire nucleus or macula of the germinal vesicle has remained undivided, and it has been supposed that it has of itself constituted the germ of the embryo-cell, which afterwards occupies the centre of the first segmenting mass of the yolk, and whose progeny by division exists as nuclei in the interior of the successively increasing segments of the cleaving germinal portion of the yolk. A recent observation by J. Müller seems to lead the way to a different view of this phenomenon. He has observed * in one of the Mollusca, the Entoconcha mirabilis, that the germinal vesicle does not disappear or undergo a change at the time of the maturation of the ovum, but remains discernible as the foundation of the clear *embryonic-cell* which occupies the centre of the yolk mass when segmentation is about to take place. Remak † has been led, by his observations on the Batrachian ovum, to

* The observations of Bischoff had long ago shown that in the periodical dehiscence of ova which accompanies the heat of female quadrupeds, the ova may be detected, though unfecundated, in the course of their descent through the Fallopian tubes and uterus (Periodische Losreifung, &c., 1842), and some observations appear also to have shown that the same is the case in the human female at the periodical return of menstruation. (See a paper by H. Letheby, M. B. in the Philos. Trans. for 1851, p. 57., where two cases are described in which ovules or their remains were detected in the Fallopian tubes of unimpregnated women who had died at or about the menstrual period.)

* Archiv. der Physiol. 1852. Leydig in the same.

† Untersuch. über die Entwickel. der Wirberthiere.

doubt the correctness of the view hitherto generally adopted as to the entire disappearance of the germinal vesicle in that instance, and holds it as probable that a part of it at least remains in connection with the formation of the embryonic cell. These statements are sufficient to show that the phenomena of the dehiscence of the germinal vesicle and its relation to the subsequent changes in the ovum induced by fecundation are as yet very imperfectly understood, and that the discovery has still to be made of the link in the chain of connection between the last stage of existence of the ovigerm, and the first origin of the nucleus round which the subsequent organising process of segmentation begins. But that some such connection exists, all who have made a study of this part of the history of the ovum are inclined to believe.

5. Relation of the ovum to fecundation by the male sperm.

The act of fecundation is necessary for the perfection of all true ova. In the production of gemmæ or buds, in the multiplication of nonsexual individuals, and in the various examples of Metagenesis previously referred to, the germs from which the new products arise may be nucleated cells or groups of these, and may without doubt be the descendants of the original cell-germs of ova; but for their development into the new beings produced from them, no combination, so far as is yet known, with the product of cells of a different kind, as in fecundation, is necessary. It is otherwise with all true ova. Their germs may be the descendants through the ovary of an original cell-germ, from which the animal bearing the ovary was produced; but for the generation of an ovum the ovigerm must be subjected to the influence of the sperm, and for its development there is required a new process of organisation, inaugurated by segmentation, which is the invariable consequence of fecundation, and is the first obvious change in a fecundated ovum leading to embryonic formation.

The developed form of the spermatic substance * is in by far the greater number of animals that of minute ovoid or rounded particles of various form, with each of which is connected a long and extremely delicate filament, which moves with vivacity in a vibrating or oscillatory manner when immersed in water and various bland animal solutions. There are other less common forms of spermatozoa, such as those of Crustacea and Nematoidea, which have not the filamentous appendage, and are motionless. The vibratory motion of filamentous spermatozoa bears some resemblance to that of some kinds of fine cilia, and is the most apparent indication of the active state of their vitality.†

It is now ascertained beyond doubt that in a number of animals the spermatozoa come into direct contact with the yolk substance and embryogerm, or with the internal contents of the ovum. The actual entrance of the spermatozoa into the ovum has been observed in Mammalia, Batrachia, Osseous Fishes, Insects, Nematoid Worms, some Mollusca, and Echinodermata; and there have been ascertained circumstances regarding the ova of other animals which warrant the inference that the spermatozoa enter the ovum in many more than those in which the phenomenon has already been actually observed. After long continued doubt and much discussion of this point, physiologists are therefore now generally agreed that in all instances a direct action of the spermatozoa in substance on the contents of the egg is necessary to fecundation. The manner of access of the spermatozoa to the interior of the ovum is probably various in different animals. In a few, as Trematode and Cestoid Entozoa, the sperm is mixed with the contents of the ovum, viz., the germinal vesicle and yolk, at the time when these are brought together from the separate organs in which they are formed: in some, as the Nematoid Worms, and probably also in some other animals, the sperm comes in contact with the ovum previous to the formation of an enveloping membrane; in a third set it seems probable that, as in Lumbricus, and perhaps in some Mollusca and Hirudinea, the vitelline membrane which had existed at an earlier period is dissolved or removed previous to fecundation, and the ovum or yolk substance and germ are thus left directly exposed to the action of the spermatozoa, which in Lumbricus have been observed in great numbers penetrating the substance of the yolk.

In the majority of animals, however, the sperm only reaches the ovum at a later stage of its formation, when it is already covered by the vitelline membrane or other envelopes, and through these coverings, therefore, the spermatozoa must pass to gain access to the yolk and germ. In a certain number of animals the vitelline or enveloping membrane appears to be quite entire and closed on all sides, so that, as in Mammalia, in which Martin Barry was the first in 1843 to perceive with certainty the entrance of the spermatozoa into the ovum, these bodies must in some way, not yet fully known, pass through the consistent wall of the enclosing membrane; but in other animals, as first discovered by J. Müller, a special aperture or perforation of the egg-covering exists, apparently destined to allow of the more rapid entrance of the spermatic bodies. This *micropyle* apparatus, sometimes consisting of one, and at others of a number of apertures, has now been observed in several Echinodermata, in Acephalous Mollusca, in all Insects, and in Osseous Fishes; and it is more than probable that it exists in a considerable number of other animals in which it has not yet been detected. But still, making due allowance for the probable extension of discovery in this direction, the care and accuracy with which the micropyle apparatus has since its first discovery been sought for without success in Mammalia and

* See the article Semen.

† See especially the recent researches of Kölliker on the Sperm in Zeitsch. fur. Wissensch. Zool. vol. vii.

some other animals, in which, had it been present, it could scarcely have escaped so careful a scrutiny, warrant the belief that in a certain number of animals the spermatozoa do actually penetrate the apparently entire egg-covering.

It is not my design to enter here upon the consideration of the mode and nature of the action exerted by the spermatic matter or the spermatozoa in producing the changes of fecundation. Upon this subject the reader may with great advantage and interest consult the latter part of the article Semen in this Cyclopædia by R. Wagner and Leuckart, the papers of the late Mr. Newport in several recent volumes of the Philosophical Transactions, and the learned article by Professor Leuckart on Generation contained in the fourth volume of R. Wagner's Handbuch der Physiologie. I will only remark in passing that from Mr. Newport's and other researches it appears that while the actual mixture of an appreciable quantity of the spermatic substance is necessary to induce fecundation, the extreme rapidity with which the action takes place, the minuteness of the quantity of the spermatic matter which is sufficient to induce it, and the fact now observed in a variety of instances that the spermatozoa which have entered the ovum remain apparently little changed for a considerable time after the changes of the ovum consequent on fecundation have made some progress, — lead to the conclusion that there is something in the nature of this action inconsistent with the idea that it is one of mere combination in substance of the developed contents of the male and female generative products. But whether this is to be referred to the class of "contact actions" of which themselves so little is known, or to what other kind of action it may be compared, the ascertained facts do not enable us in the least to determine. The almost universal presence of vibratory motion in the spermatozoa during the time in which they retain their fecundating power, naturally led physiologists to connect that motion with the fecundating action; but on the other hand, the occasional, though rare examples in which the spermatozoa are entirely motionless, seem sufficient to cause the rejection of the view that the force which produces the vibratory motion is identical with that which calls forth the series of histogenetic and organogenetic changes which result from fecundation.

But the consideration of this subject would lead us into the discussion of the whole question of vital forces, which in its present unsatisfactory state it is desirable to avoid. The physiologist agrees, for the sake of convenience of expression, to adopt the terms of power, property, force, &c., to denote the conditions necessary for the occurrence of certain actions or changes. He employs the term vital force merely as the indication of the supposed cause or causes of an ascertained regular sequence of vital phenomena; but all philosophical accuracy rejects the idea of any unseen separate and single force which is at work in bringing about the sequence in question. The fecundating power of the semen is an expression used only for convenience to denote the invariable sequence or relation as cause and effect which has been observed to subsist between the contact of spermatic matter with the ovum, and the changes in the latter which follow on the act of fecundation. We might with as much propriety have given a name to a separate power residing in the egg or its germ which render it susceptible of fecundation, as of a special power belonging to the semen by which that susceptibility of the ovum is acted upon. The efficient cause of the process of fecundation can only be educed, as in all physical as well as vital changes, from a perfect knowledge of all its phenomena, and the statement of the efficient cause of such actions is only the expression of the most general and best known law to which a full acquaintance with the phenomena enables them to be reduced. Fecundation is to be regarded as a purely vital change, seeing that it takes place only in the usual conditions of vitality; but, like all other vital changes, it appears more probable that a variety of conditions of the organic matter rather than any one known property or condition are necessary for its occurrence.

In endeavouring to deduce the most general phenomena which accompany this remarkable change, it may be said that fecundation consists essentially in the mutual action of two different organised bodies, which are respectively formed from two different cells; the ovigerm and the spermgerm. If we may form any general conclusion from what may be so well observed in Nematoid Worms, the development of the ovum and the spermatic cells from their respective germs is remarkably similar, for in both the internal cell is developed from a minute molecule from within, while the external part is deposited from without. The spermatozoa are formed in connection with the nucleus or nuclei of the sperm-cell; and the germinal part of the ovum, though it consists mainly of the granular part of the yolk, which is directly formative, very probably comprehends also in some shape or other the effused contents of the germinal vesicle. In this way, then, we may conjecture that in the act of fecundation the products of the original cell-germs meet and combine or mutually influence each other. The cell-germs, then, are the links in the chain of organic connection between either or both the parents and the progeny capable of being developed from the fecundated ovum. Such a view, though still in a great measure speculative, seems to be in accordance with the facts known as to the perfect transmission of the structure and qualities of either or of both parents to the offspring.[1]

6. Immediate effects of fecundation on the ovum; segmentation, and first changes of the ovum related to the commencement of embryonic development.

It does not come within the scope of the present article to describe in detail the process of fecundation, or the phenomena which follow it, but it may be proper to state here in a general way the relation which subsists between the earliest changes occurring after fecundation, and the commencement of those phenomena of a histogenetic nature which precede the formation of the embryo itself. The most obvious and constant of these changes is that known as the cleavage or segmentation of the yolk, — a process which has been observed in the ova of all animals, and is not less interesting from its own nature, than from the bearing of its phenomena upon the explanation of the earliest organising process of embryonic development, and upon the whole subject of histogenesis.

The segmentation affects only that part of the ovum of animals which is directly germinal or formative; and it results in the production of that layer of organised cells, of variable extent, in the centre of which, in a determinate position and direction, the rudiments of the embryo are first formed. The process of segmentation is, therefore, the prelude to the formation of the Blastoderma or germinal membrane of Pander.

The extent, therefore, to which segmentation affects the yolk differs greatly according to the amount of the yolk-substance which is directly germinal; that being in some animals the whole, and in others only a fraction of the yolk, in proportion to the part which is only indirectly nutritive. In that group of ova, then, to which those of Mammalia belong, and which we have called the small-yolked, the entire yolk, or, at all events, its superficial layer, being directly formative, or being involved from the first in the production of the Blastoderm, the segmentation is complete, or the process of cleavage affects the whole mass of the finely granular yolk within the zona or vitelline membrane. In those ova again, such as we find in the bird among vertebrate, and the cuttlefish among the invertebrate animals, in which the formative yolk has the most limited extent, and consists only of a finely granular disc near the surface of the much larger mass of the cellular nutritive yolk, the segmentation is confined to that disc alone, and is therefore, in some respects, widely different from that which occurs in Mammalia. In the intermediate group of ova belonging to Batrachia and Osseous Fishes, there are many gradations of transition from the complete to the partial cleavage, so that in some, as the common frog, it is nearly, but not entirely, over the whole yolk; while in others, as in the salmon or osseous fishes, it does not extend over more than a third of the surface of the yolk.*

In the greater number of instances there is recognised in the mass of the whole yolk, or in its germinal part, immediately previous to its undergoing segmentation, a clear simple cell, generally nucleated, which was not before perceptible; to this the name of *embryo-cell* has been given, in order to distinguish it from the germinal vesicle, from which it has hitherto been believed it is in some measure distinct. In other instances a clear spherule or space only is observed in the place of the embryo-cell, and in a few animals no clear part of this nature has yet been detected. The division of the embryo-cell accompanies, or rather immediately precedes, that of the germ-yolk, so that each mass formed by the cleavage, grooving, or segmentation, as the case may be, contains as its nucleus or centre an embryo-cell, or clear spherule of its own, descended from the first cell or spherule of the same description.

The process of segmentation, whether it involves the whole ovum, or is limited to a larger or smaller disc of the yolk, proceeds in most animals with a certain degree of geometric regularity, so that the number of germ-yolk segments are successively multiplied so as to be in the numbers 2, 4, 8, 16, 32, 64, &c., until by the ultimate division a vast number of small globular masses are formed, which occupy principally the surface of the yolk over all its germinal portion.*

The last result of the segmentation is the production of the blastoderma or germinal membrane in which, by other changes, the rudiments of the embryo subsequently make

* The more important phenomena of the yolk-germ cleavage or segmentation have been ascertained principally by the following observations: viz. 1st. of Prevost and Dumas in Batrachia, as early as the year 1824, and subsequently of Rusconi and Von Baer in the same animal; 2nd. of Bischoff and Barry in Mammalia, in 1838–39, their observations being confirmed by myself in 1840, and greatly extended by Bischoff before the publication of his work upon the development of the rabbit, in 1842; 3rd. of Bagge in 1841, and of Kölliker in 1843, on Nematoid Worms; 4th. of C. Vogt in the Salmonidæ and in the Alytes Obstetricans in 1842; 5th. of the same author, of Quatrefages, and many others in various invertebrate animals; 6th. in its most limited form the phenomenon was first well described by Kölliker in Cephalopoda in 1844; and 7th. in birds by Bergmann in 1846, by Coste in 1848, and by myself in the following years. The observations on this subject are far too numerous for quotation; those especially which have been made in experiments by artificial fecundation are most favourable to the investigation of the segmentation and other phenomena which follow immediately on fecundation. And in all these instances, as well as in very numerous others, the occurrence of segmentation and the regularity of its phenomena are so constant that we may regard it as one of the best established series of facts in organic nature. The observations with regard to segmentation in the ova of insects, which are still imperfect, form the only exception to the foregoing statement with which I am acquainted.

* Reference is here made chiefly to the best-known and most common kind of segmentation, in which this process consists in the massing of the granular and fluid substance of the yolk round the embryo-cells or clear spheres as centres; but it is right to state that there is another form of this process, as yet only observed in some of the Cestoid and Nematoid Entozoa, in which the yolk, either clear or granular in its structure, does not appear to follow the divisions of the embryo-cells, but the gradually increasing progeny of the latter assimilate or combine more and more with the yolk, so that at last, when the germinal part of the ovum is entirely occupied with new cells, the original yolk has quite disappeared. The nature of this process, as compared with the more common form of yolk segmentation, is not perhaps as yet fully understood.

their appearance. According to most ovologists, the last globules formed by segmentation are the nucleated organised cells immediately constituting the blastoderma. A different view of the process, however, in Mammalia, has been taken by Bischoff, very decidedly set forth in his two most recent works on the development of the guinea-pig and the deer; according to which the last resulting spherules formed by segmentation are not true cells, and that previous to the formation of the blastodermic cells, the yolk-germ falls completely into an amorphous or homogeneous finely granular substance, out of which, secondarily, the blastodermic cells are produced by a process of cytogenesis. It seems probable that, in the different classes of animals, there may be considerable variety in the degree of perfection in organisation or advance in cell-structure to which the segments of the yolk have attained at the period when the development of the embryo begins to manifest itself. But in the higher animals at least the weight of evidence appears to me in favour of the view that the process of segmentation results directly in the formation of blastodermic cells. The fact now established by the observations of Reichert in Entozoa, in 1841, of Ransom in osseous fishes, and more particularly those of Remak in Batrachia, that a delicate membrane is formed over the surface of each of the segments as they appear, and that the last and smallest segments possess a delicate membranous envelope, appear to show that, in these animals, each segment has the structure of an organised cell, and is very similar to, if not identical with, those of the blastodermic lamina.

The origin of the embryo-cell is still involved in obscurity. Most ovologists are disposed to connect it in some way or other with the previously existing germinal vesicle, or some part of its contents, and more especially the nucleus. For the solution of this question, as already remarked, a more accurate knowledge of what happens to the germinal vesicle at the time of that disappearance which has been so commonly observed at the period of the maturation of the ova of almost all animals, will be required. Does the macula remain, as has been alleged by some, to form the nucleus or the whole of the embryo-cell? Or, in other cases, if the multiplied maculæ are dispersed among the granules of the germinal yolk, are they again collected together into a mass or spherule to form the embryo-cell? Or, again is the embryo-cell formed out of other materials, and not necessarily either partially connected with, or wholly derived from, the germinal vesicle? And finally, might it not be, according to some recent observations, such as those of J. Müller on Entochoncha and those of Remak on the frog, that the disappearance of the germinal vesicle is not attended with the dispersion of its contents, but is a phenomenon caused only in a certain number of animals by the solution of the delicate external wall of the vesicle, and by some change in the position and consistence of its contents? Further observations will be required to determine this point; but if in the meantime we regard it as most probable that the embryo-cell is in some way or other connected in its origin with the germinal vesicle, we might further found upon this the speculative view that the blastodermic cells and the blastema from which unquestionably, by a histogenetic process of cell-division and multiplication, the various textures and organs of the animal body are produced, may be regarded as the descendants of the original cell-germ from which the ovum was developed combined with the sperm. We should thus trace the organic cellular connection between the succession of parents and offspring, which I have stated to be one of the most general facts in organised nature.

The observations respecting the very remarkable movements of the yolk, before and during the earlier stages of the segmenting process which have now been recorded by several physiologists, must excite the liveliest interest, and suggest subject for much reflection as to the evidence they may afford of the causes of this change, or, if we may use the expression, of the forces by which segmentation is brought about. There seems to be little doubt that the embryo-cell (and its nucleus first of all) is the earliest to become divided, and that the process of cleavage then proceeds from the surface of the segmenting mass inwards towards the cell; but in what relation the nucleus, granular substance of the yolk, and ovicell-membrane stand to each other in this process, must be left to be determined by future researches.

Of the other early changes in the ovum which immediately follow fecundation and precede embryonic development little need here be said. They consist principally in the greater degree of consolidation and compactness acquired by the germinal part of the yolk, and in the formation in most animals of a clear space between the surface of the yolk-substance and the enclosing vitelline membrane. It is in this clear space, or, as it has been called by Newport, respiratory chamber, that the spermatozoa have been observed in those instances in which they have been ascertained to penetrate into the cavity of the ovum. There is another phenomenon of the same period, which has now been so frequently observed, and which is of so peculiar a nature, that it must not be passed over without notice; I allude to the appearance in the respiratory space of one or more clear and highly refracting spherules, nearly of the size of the germinal vesicle, but quite independent of it. These clear hyaline-like globules have been observed in the ova of Gasteropodous Mollusca after fecundation by almost all those who have attended to the ovology of this class of animals, among whom may be mentioned Dumortier, Pouchet, Van Beneden, Nordmann, and Vogt; in the Annelida by Quatrefages; in Mammalia by Bischoff and Barry; and in Batrachia by Newport. From the observations of Quatrefages in Hermella they appear to be excluded or expressed, as it were, from the clear basement-substance of the yolk; and Bischoff states that they gradually disappear, or are dissolved without obvious change. We are at a loss to determine what office these globules may have in connection with the changes of the ovum at the time they appear.

Lastly, I would notice the interesting relation which appears to subsist between the situation of the germinal vesicle and the centre of the germinal membrane afterwards formed, or the germinal pole of the ovum, and the conformity in the direction of the line of the first cleavage of the yolk with that of the principal axis of the embryo in vertebrate animals. The first fact has been observed in all animals, and the latter has been ascertained by Mr. Newport's researches in Batrachia, and by observations which I have myself made in the bird's egg during its descent through the oviduct. These facts, as yet inscrutable in their nature, point to interesting laws relating to the connection of the first phenomena of development, which may be worked out by the further prosecution of these inquiries.

In the preceding part of this article we have considered chiefly the anatomical structure of the ova of animals, and have made little mention of their chemical composition. The knowledge of the latter subject is as yet very imperfect. In a recent Memoir* Messrs. Valenciennes and Fremy have given an account of an extended series of experimental researches in which they have been engaged, with a view to determine the differences in the chemical composition of the ova of different animals, and although this investigation is still necessarily incomplete and fragmentary, they appear already to have arrived at some interesting results. The following are some of the more important of these results.

The albumen or white is not exactly of the same composition in the eggs of different birds; but it generally contains albumen with salts and a compound of sulphur in solution. In the yolk of birds' eggs they recognise the principle first distinguished by Dumas and Cahours as *Vitelline*, a substance precipitable by mixture with a large quantity of water, and apparently more nearly resembling fibrine than albumen in its composition and some of its properties. The phosphuretted fat of the yolk is somewhat similar to the cerebral fatty matter.

The glairy white of the eggs of cartilaginous fishes is very different from that of birds' eggs, being neither soluble in water nor coagulable by heat nor acids to the same degree. It seems to contain only traces of organic matter. The angular and tabular particles of the yolk of cartilaginous fishes are composed of a principle which these authors regard as peculiar, and have named *Ichthine*. This substance is insoluble in water, alcohol, and ether, and, on being dissolved by hydrochloric acid, gives no violet colour, as albumen does. It is dissolved by all the concentrated acids, and by dilute acetic and phosphoric acids. Its composition is stated to be as follows: carb. 51; hyd. 6·7; nit. 15; ox. 25·4; phosph. 1·9.

* See Journal de Pharmacie, &c., vol. xxv. pp. 321. and 415., and vol. xxvi. p. 5., 1854.

In the ova of osseous fishes these authors do not find the same organic principle, but have detected two others in variable proportions. One of these, which they have named *Ichthidine*, exists only in small quantity, and is absent in some fishes: it is quite soluble in water. The other which is more generally prevalent and in larger though variable quantity is precipitated by water into a viscous substance. This has been named *Ichthuline*. Messrs. Valenciennes and Fremy have ascertained the interesting fact that while these principles, especially ichthuline, exist in large quantity in the ova at an early stage of their growth in the ovary, they gradually diminish in quantity or are changed as the ova approach maturity, and give place chiefly to albumen, which holds the phosphuretted fat in suspension. In the salmon's egg there is a large proportion of ichthuline, which is the cause of their becoming opaque when water enters the yolk. These authors propose indeed this character as a test of the maturity of the ova, as they are not rendered opaque by water when mature. It would be interesting to know whether fecundation produces any immediate chemical change on the principles of the yolk. The composition of ichthuline is stated to be as follows: carb. 52·5; hyd. 8; nit. 15·2; ox. 22·7; phosph. 0·6; sulph. 1.

The ova of Batrachia seem to resemble most nearly those of cartilaginous fishes, in so far that the tabular particles of the yolk are composed of ichthine. The external gelatinous covering is described as a tissue of hyaloid membrane which absorbs water in a determinate quantity.

The ova of Ophidia and Sauria resemble nearly those of birds in the composition of the white and yolk, containing the principle vitelline in the latter. The yolk of the Viper presents the singular peculiarity of becoming gelatinous by immersion in water.

In the ova of several Chelonia they have detected a different principle from vitelline to which they give the name of vitelline. This principle is soluble in potash, and has the following composition: carb. 49·4; hyd. 7·4; nit. 15·6; ox. and phosph. 26·7.

Among the invertebrate animals Messrs. Valenciennes and Fremy have examined the ova in several classes. In the Crustacea they have given much attention to the investigation of the curious colouring principle of the ova, which appears to be the same as that existing in the shell, and which being green in the moist state passes into red in a variety of circumstances. They have isolated this colouring matter by a very simple process, and give an interesting account of its properties, especially of the circumstances causing it to change to red, such as the action of alcohol, boiling, desiccation, placing in a vacuum, friction, &c.

The ova of Arachnida and Insects are

quite different from those of Crustacea in their composition, containing albumen, fatty matters, and a large quantity of a substance precipitable by water.

The ova of Mollusca differ greatly in composition from those of other animals: more particularly in the entire absence of fat from them.

From these researches it appears that there are considerable differences in the chemical composition of the ova of animals of different great groups, and even among those not far removed from each other in the zoological scale, and that there are also considerable differences according to the state of advancement of the ova of the same animal, more especially it would appear that a marked change of composition takes place at the period of complete maturity. The researches referred to appear to have brought to light several new organic principles which are modifications of albumen or belong to the same class, and which may be considered as *Vitelline principles* as belonging to the yolk of different animals: such are Vitelline, Ichthine, Ichthidine, Ichthuline, and Emydine.

The full citations of different works and memoirs on the subjects of this article render it unnecessary to give any detailed bibliographical list at its termination. I may, however, call the attention of the reader to the following works already cited, as forming the principal basis of modern knowledge of ovology and development, viz.: The Inaugural Dissertation of *Pander* on the Development of the Chick, published in 1817. The History of the Egg before Impregnation, by *Purkinje*, in 1825. The Epistola of *Von Baer*, in 1827. The contributions of *Von Baer* and *Rathke* to *Burdach's* Physiology, in 1827 and 1828. The various Memoirs by *Rathke* at different times, and *Von Baer's* Lectures on Development, completed in 1837. The Systematic Manual of Development by *G. Valentin*, in 1835. The Prodromus and contributions by *R. Wagner*, in 1836. and the Manual of Physiology by the same author. *J. Müller's* Physiology, and especially the English translation of the more recent edition. The researches of *Martin Barry*, in 1838 and 1839. The various contributions of *Bischoff*, beginning in 1838: His Systematic Treatise on Development in 1842, and his Monographs on the Development of the Rabbit in 1842, of the Dog in 1845, of the Guinea Pig in 1852, and of the Deer in 1855. The researches of *Coste* beginning in 1833; his work on Comparative Embryology in 1837, and his large and beautifully illustrated work, as yet unfinished, beginning in 1850. The works of *C. Vogt* on the Alytes Obstetricans (Batrachia) and on the Embryology of the Salmonidæ, in 1842. Lastly, the recent and valuable researches of *Remak* on the Development of Vertebrata in 1853–1855; and the republication of *R. Wagner's* Icones Physiologicæ by *Ecker*. The works relating to the invertebrate animals are much too numerous for quotation. I will only mention the researches of *Kölliker* on the Cephalopoda, of *Quatrefages*, *Vogt*, and others on the Mollusca, Annelida, &c., and those of *J. Müller* on the Echinodermata.

I would also refer the reader to the excellent report on the progress of discovery in regard to the Ovum by *Thomas W. Jones* in the Brit. and For. Medical Review for Oct. 1843, to *Bischoff's* article on the History of Discovery in Development, and its application to the explanation of Malformations in *Wagner's* Dictionary of Physiology, to *Leuckart's* Article on Generation in the same work, and to *Vrolik's* Memoir on the Explanation of Monstrosity from the History of Development, and to his article Teratology in this Cyclopædia. A large amount of information on the whole of our subject will also be found in *C. Vogt's* interesting Letters on Living and Fossil Animals in 1851; in *Victor Carus's* System of Animal Morphology in 1853; in *Van der Hœven's* Manual of Zoology, with additions by *Leuckart* in 1850–1856; and in the English works of *Carpenter*, *Owen*, and *Rymer Jones* on Comparative Anatomy and Physiology.

In now bringing this article to a close, the author owes an apology to the conductors and the readers of this Cyclopædia for the extreme tardiness with which it has appeared. The delay has arisen, in part, from personal circumstances which need not be mentioned here, and in part from the nature of the subject of which the article treats. In the original plan of the article, it was intended that it should comprehend, along with the history of the ovum, an account of the development of the embryo. But as time advanced, and every successive year added new and important matter to our knowledge of the science, and greatly modified the statement of facts previously regarded as established, it became more and more difficult, especially in the hands of one interested in the experimental investigation of many of the individual facts, to present a systematic and at the same time clear and brief description of the researches of physiologists on the subject of development. The author regrets deeply that he should thus be prevented from furnishing the readers of the Cyclopædia with this part of the article as originally intended. But at the same time he believes that when the recent rapid progress of many departments of the subject is considered, and the vast number of details which would be required to embrace even the shortest account of the origin and formation of all the textures and organs of the animal body, the knowledge of which forms a science that is coextensive with the whole range of anatomy and physiology, it may be thought that he has in present circumstances judged rightly in abandoning the attempt to compress into a limited space the statement of so extensive and important a branch of physiological inquiry.

(Allen Thomson, M.D.)

PANCREAS (Πάγκρεας*, Gr.; *Pancreas*, Lat.; *le Pancréas*, Fr.; *die Bauchspeicheldrüse*, Germ.; *Pancrea*, Ital.). The pancreas is an azygous, non-symmetrical, glandular organ, possessing a duct, and, therefore, belonging to the category of *true glands;* connected anatomically with the alimentary canal, and physiologically with the function of digestion.

On taking even the most superficial and general view of this organ, two or three things cannot fail to strike the attention: one is, the close affinity and strong contrariety which it at the same time displays to the salivary glands†—affinity in point of appearance and structure, being, like them, a typical representation of a conglomerate gland,—contrariety in point of situation and function, the one being placed at the very threshold of the alimentary canal, the other at an advanced position in it; the one acting on raw material, and having in part at least a mechanical use‡, the other having to do with material far gone in the process of assimilation, and possessing a function, whatever it *may be*, certainly *not* mechanical in any degree.

Another striking circumstance is its wide diffusion. It exists in all vertebrata;—mammalia, birds, reptiles, and most fishes, all possess a pancreas, and that quite independent of what the nature of their food may be, animal, vegetable, or mixed; a fact that one would have imagined would itself have prevented the adoption of the old views with regard to its function.

Another circumstance, not less striking, is its constant relation to the duodenum: whatever may be the other modifications of the alimentary canal, from the straight and simple tube of some carnivora to the voluminous apparatus of the vegetable feeders, or whatever may be the modified form of the pancreas itself, still, if the organ exists, its relation to the duodenum is invariable; if there is a duodenal fold, it is placed in it; and if there is not, it makes the closest approximation to an analogous position that is possible: indeed the uniformity of this relation is so invariable, even under circumstances where it would appear to be indifferent, that one cannot but regard it as one of those instances of conformity to type in which uniformity appears to exist for uniformity's sake.

The arrangement of the subject of this paper that most naturally suggests itself, is to treat first of the structure, and then of the functions of the organ. I shall therefore arrange my observations under the following heads:—

1st. The descriptive anatomy of the human pancreas, including an account of so much of its structure as may be made out by a naked-eye examination.

2nd. Its minute or general anatomy.

3rd. Its comparative anatomy, including those modifications both of the form and ultimate structure of the gland that the animal series exhibits.

4th. The physiology of the pancreas,—the *rôle* that it plays in the function of digestion.

Lastly. A short account of some of the most striking pathological changes that the organ is liable to.

I. Human Anatomy.

Situation.—The pancreas is so placed that for its display it is necessary to open the cavity of the great omentum. This may be done either by dividing the gastro-hepatic omentum and depressing the stomach, or by detaching the gastric layer of the epiploon and turning the stomach up, or by dividing the transverse mesocolon and turning up both transverse colon and stomach. In either of these ways the cavity of the omentum is opened, and the organs concealing the pancreas are removed.

Placed transversely across the upper part of the abdominal cavity, and closely applied to its posterior wall, the pancreas extends from the duodenal fold on the right to the hilum of the spleen on the left, across, therefore, the epigastric into both hypochondriac regions. It is not perfectly transverse, however, but extends from the right a little upwards as well as to the left; it corresponds to the level of the first and second lumbar vertebræ and to the splitting of the two laminæ of the transverse mesocolon: it is post-peritoneal, being invested by that membrane only on its anterior surface.

Relations.—By its right extremity it is closely engaged in the curvature of the duodenum, to the inner border of which it is intimately attached, and which it often receives into a groove more or less deep, formed by a projection of the gland to a slight extent on the anterior and posterior surface of the intestine. Sometimes this groove is very slight, and the relation of the margins of the gland and intestine merely that of apposition; at others, the inner margin of the duodenal fold will be deeply imbedded in the gland substance, the projection both in front and behind being considerable. More frequently, however, the gland trespasses much further behind the intestine than it does in front, so much so occasionally as to separate it in a great degree from its posterior relations. The structures on which the posterior surface of the pancreas rests are, the vena cava, the bodies of the vertebræ, the aorta, the crura of the diaphragm, the left kidney, its supra-renal capsule and renal vessels, the lower part of the solar plexus with the commencement of the plexuses thence proceeding, as the aortic and superior mesenteric; the splenic vein passing from left to right, the superior mesenteric vein and artery, the vena portæ, the common bile duct, many lymphatic vessels and glands, and the commencement of the thoracic duct and vena azygos. To all these structures it is intimately attached by cellular tissue, and to the irregular surface which they form it is, as it were, moulded or modelled, so that when it is care-

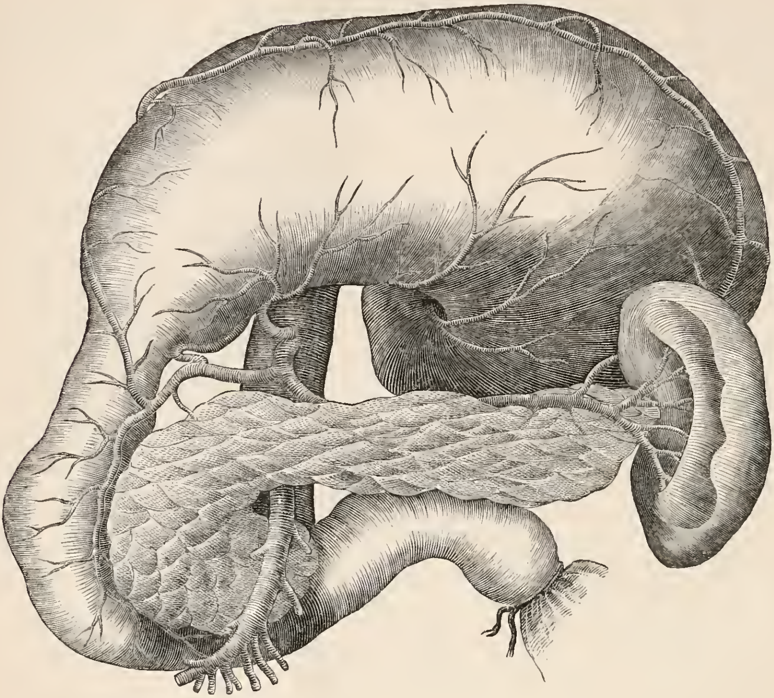
* παν κρεας, all flesh.

† This striking resemblance suggested to the older anatomists the name of "salivary gland of the abdomen," an appellation first given to it by Siebold.—Historia Systematis Salivalis.

‡ See Bernard's experiments on the secretion of saliva.

fully dissected away, it presents eminences and depressions corresponding to them, as, for instance, the longitudinal furrow occupied by the splenic vein, and the deep groove in

Fig. 54.



Human Pancreas, shown in situ *by throwing up the stomach.* This drawing was taken from a young subject in which the curvature of the head of the pancreas, following that of the duodenum, was particularly well shown.

which the superior mesenteric artery and the vena portæ are received.

In front it is in relation with the posterior surface of the stomach, which rests on it when empty (tanquam pulvinar, *Sœmm.*), and moves freely upon it; but when this organ is distended with food, it recedes from it, and its lesser curvature comes into more immediate relation with the gland. In cases in which the stomach is situated lower down than usual, as in emaciated individuals, where a great part of the small intestine occupies the cavity of the pelvis, the pancreas comes into relation in front either with the liver, or with the anterior wall of the abdomen, from which the gastro-hepatic omentum alone separates it, and through which it may be easily felt. This disturbance of the normal relations always exists, according to Cruveilhier, whenever the vertebral column can be felt immediately behind the walls of the abdomen. The pancreas is also in relation, in front, with the angle formed by the ascending and transverse colon and with the commencement of the duodenum.

The upper border is in relation with the splenic artery, for the reception of which it is grooved, and which often runs in a canal formed in the substance of the gland through its entire length; it is in relation also with the Spigelian lobe of the liver, with the first portion of the duodenum, and the cœliac axis.

The lower border is bounded by the inferior horizontal portion of the duodenum, from which it is separated, near the middle line, by the superior mesenteric vein and artery, which notch it, and which also separate it from its reflected portion or head.

The right extremity is engaged in the duodenal fold in the manner described, and is in relation with the ductus choledochus. From the intimacy of its attachments to the duodenum, it always accompanies this intestine in its displacements, so that when the duodenum is situated lower down than usual, which happens in displacements of the stomach downwards, the head of the pancreas is always removed in the same direction.

The left extremity is in relation with the left kidney, and with the spleen upon which it is sometimes flattened and blunted, and sometimes slightly enlarged, and to which it is attached by the intervention of the splenic veins, which send many branches into its substance: sometimes it does not extend quite so far as the spleen by half an inch or an inch.

Shape.—From its elongated form, the pancreas has been described by anatomists as possessing a body and two extremities; and of these extremities one, which is enlarged and clubbed, has been called the *head;* the other, tapering and acuminated, has been called the *tail;* the middle portion, the great mass of the gland, being the *body:* other describers* have suppressed the body altogether, and described as the tail all that portion which is not included in the curved intumescence at the right extremity, which they designate the head. Indeed the imaginations of anatomists have been largely drawn on to supply analogies whereby to illustrate the shape of this organ. Some have compared it to a hammer,—some to a dog's tongue; among them all I think the best is that which compares it to a pistol.

But, passing by these fanciful resemblances, the pancreas, from its transverse elongation and antero-posterior flattening, presents for description a right and left extremity, an upper and lower border, and an anterior and posterior surface; and these parts I shall describe in succession in the order in which I have mentioned them.

The *right extremity*, to which the name *head* has been assigned, is that portion which is engaged in the duodenal curvature, and to which, from its occasional separation from the rest of the gland, the name of *lesser pancreas* has also been given†: it differs from the rest of the gland in being thicker and more massive, curved instead of straight, and situated on a more posterior plane. It is thus formed:—when the pancreas, in passing from left to right, has arrived at the duodenum, it becomes closely attached to that viscus, and follows its course, first downwards, and then to the left, passing by its extremity, behind the superior mesenteric vessels, for which it thus forms a sort of groove or channel. It is by the fusion and massing of this curvature that the head is formed; but in very young subjects, and in the lower animals, the curvature of the pancreas is as conspicuous as that of the duodenum, and by separating it from its attachments, and straightening it out, all appearance of head vanishes, and it becomes a long prism, or flattened cylinder of even thickness throughout.

In the human adult, however, it is impossible thus to unravel and straighten the right extremity; and the fusion of the parts has often proceeded to such an extent as entirely to obliterate the original curvature, the groove for the vena portæ and superior mesenteric vessels being the only trace of its concavity.

The *left extremity* gradually tapers, getting both narrower and thinner; it is sometimes bifurcated, sometimes blunted and flattened against the spleen, and sometimes slightly enlarged; it presents nothing for special description.

The *upper border* is much thicker than the lower, so much so, that some anatomists have described the gland as being prismatic. In the middle the cœliac axis rests upon it; to the right the hepatic artery and first portion of the duodenum are in contact with it, and to the left it is deeply grooved by the splenic artery.

This groove does not run along the top of the border, parallel to it, but crosses it obliquely from behind forwards as it passes to the left extremity, curving over it, as it were, so that while the commencement of the artery is behind the pancreas, its terminal branches are in front (see *fig.* 54.). Sometimes this groove is converted into a canal, by the gland closing over it.

The *lower border*, much thinner, is tilted rather forwards to the right, by the passage of the superior mesenteric vessels beneath it, which separate it from the third portion of the duodenum; on the left the inferior mesenteric vein passes beneath it to join the splenic.

The *anterior surface* looks upwards as well as forwards, and is convex both transversely and longitudinally; it is the only portion of the gland that is covered by peritoneum: from this circumstance, as well as from its being the free surface, it is very smooth.

The *posterior surface* contrasts strongly with the anterior, for being uncovered by peritoneum, and closely applied to all those structures against which it lies, it presents many irregular elevations and depressions, corresponding with the uneven surface which these structures contribute to form.

Size and weight.—The size and weight of the pancreas are liable to great variety, and hence different authors have stated them very variously. Wharton* gives its weight as five ounces; Meckel, from four to six; Cruveilhier states its limit as six ounces, but thinks that a healthy pancreas may be as small as two ounces and a half; Sœmmerring also considers six ounces a maximum, but carries his minimum as low as an ounce and a half. According to Krause and Glendinning, its usual weight is from two and a quarter to three and a half ounces. Its size is stated by Meckel as six inches long and one thick; Ellis gives its length as seven inches; Quain and Sharpey, from six to eight inches, with an average breadth of an inch and a half; according to Wharton, its length is about five inches, its greatest breadth one and a half, and its thickness one inch. Of all these weights and measurements I think that of Wharton, which is the earliest, comes nearest the truth; only his measurement of length is too little. From a large number of observations I find the average weight to be from four to five ounces, the length seven inches, the greatest breadth an inch and a half, and the thickness three quarters of an inch. It is smaller in women than men, but only in proportion to the difference of size. Sœmmerring says† that it is proportionately larger in the fœtus and the new-born infant

* Meckel, Manuel d'Anatomie.

† Some anatomists, as Professor Ellis, make the *head* synonymous with the lesser pancreas, independently of this separation.

* Adenographia, p. 72.

† "In nondum nato homine et brevi adeo post partum, majus pro corporis mole videtur quam in adulto." Corp. Hum. Fab.

than in the adult; a statement that my own frequent observations have verified.

The specific gravity of this gland, according to Muschenbroeck*, is, compared to water, as 2029 to 1000.

General appearance.—The best view of the external appearance of the pancreas is obtained on its anterior surface where it can be seen, through the peritoneum covering it, without any disarrangement of its structure. It is seen to be of a pale, clear, flesh colour, in which it strongly contrasts with the white cellular tissue investing it, with the yellow fat with which it is often surrounded, and with the grey and dingy coloured absorbent glands which lie contiguous. On looking more closely, it is seen to be mapped out into lobules, and this mapping out is sometimes more conspicuously marked by the septa of areolar tissue that separate the lobules being loaded with fat. The lobules are of very various shapes and sizes, from an eighth to three quarters of an inch in diameter, closely packed so as to fit into one another, and presenting an even general surface. But on a closer examination we see that these lobules are themselves subdivided by less conspicuous septa into a great number of smaller lobes; and these again, especially if assisted by a little separation with a fine knife or needle, are seen to consist of numerous minute granules, or acini, as they are termed, which, as far as the scrutiny of the naked eye goes, appear to constitute the ultimate structure of the gland; but, as we shall see more fully presently, the microscope shows these in their turn to consist of aggregations of follicles, and therefore to be truly compound. Thus a mere inspection of the external surface of the pancreas gives an indication of its internal structure; we see the acini by their aggregation constituting the lobules, the lobules the lobes, and the lobes the whole organ; the association by which these parts are bound together being more and more intimate as we descend from the greater to the less; but all of them, even the smallest, that come under the cognisance of the unassisted vision, being truly composite: this is a common character, and indeed a general description, of all conglomerate glands. The pancreas in consistence is moderately firm, the lobules having a considerable degree of hardness, but the whole gland having a certain laxness about it, from the way in which the lobes are hung together by areolar tissue.

There is no proper capsule to the pancreas: the areolar tissue which invests it does so very unequally in different parts, and is strictly continuous on the one hand with that which attaches it to neighbouring parts, and on the other with that which penetrates between its lobules to the internal parts of the organ. On the anterior surface this areolar tissue is so deficient that the structure of the gland is in no way concealed by it.

Internal structure.—On cutting into the pancreas, we see that it is the same throughout its mass as it is on its surface; that it is solid and homogeneous; that one part exactly resembles another; that there is the same aggregation of the acini into lobules and of lobules into lobes, and the same nesting in capsules of areolar tissue by the elasticity of which the acini and lobules are made to protrude from the cut surface, whereby it becomes granulated and nodular; and this irregularity of surface is almost the only difference between the appearance of a section and that of the external surface as just now described. A good idea of the absolute and relative size of the different elements may be obtained by a section: the lobes may be said to have an average diameter of $\frac{1}{3}$ of an inch; the lobules $\frac{1}{12}$, or $\frac{1}{4}$ of the lobes; the acini $\frac{1}{70}$ of an inch*; but all the measurements are liable to the greatest variety.

The areolar tissue, less abundant than in the salivary glands, consists almost entirely of the white fibrous element, and the areolæ are very lax and large: it is most abundant near the centre of the gland around the duct, and about the head of the pancreas, where it forms a firm and intimate union between the gland substance and the duodenum.

The duct of the pancreas, which has been called the canal of Wirsung, from its discovery by that anatomist in the year 1642, passes from left to right throughout the entire length of the organ, beginning within a few lines of its splenic extremity, by the union, at an acute angle, of two or more minute ramusculi, and emptying itself into the duodenum at or near the junction of its vertical and inferior-horizontal portions. Its course is somewhat sinuous; it lies, on the average, about equidistant between the upper and lower margin, but nearer the posterior than the anterior surface. It is altogether concealed by the gland structure, even its point of entrance into the wall of the intestine. After originating in the manner described, it receives continuously in its course small branches which enter it at right angles, and which, unlike the main duct, are perfectly straight and not sinuous, and mostly single and unbranched, each coming from its own appropriate lobe, without receiving any accessory branches from neighbouring ones; so that they look, as Cruveilhier has said, like the legs of a centipede, of the which the main duct forms the body. By these tributary ducts the calibre of the main canal is gradually increased till it reaches a diameter, at the right extremity of the gland, of $\frac{1}{8}$th of an inch. It is of an opaque white, and therefore easily distinguishable from the gland substance. Its walls are thin and elastic, but dense and firm. In the tenuity of its walls it stands in strong contrast with the ducts of the salivary glands; but, like them, it is continuous, by its external loose fibrous coat, with the areolar tissue of the gland. Just before entering the intestine the duct com-

* Introd. ad Philosoph. Natur., p. 556.

* This last measurement is taken from the rabbit, as it is difficult to isolate the acini of the human pancreas, or to take their measurement *in situ*, without isolation; but the measurement in the human subject very nearly approaches it.

monly receives a large tributary branch, often nearly as large as itself, coming from the head of the pancreas. This occasionally remains permanently distinct, and opens into the intestine by a separate orifice (see *fig.* 55. B, *c*), a condition always present, according to

Fig. 55.

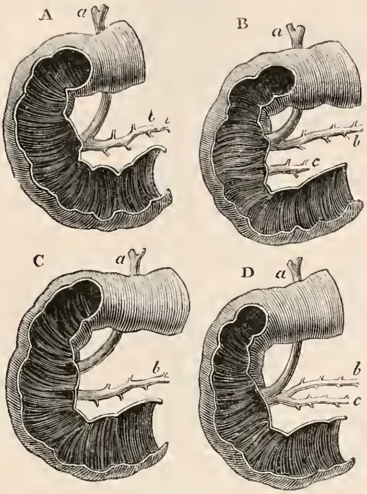


Diagram of the principal Varieties to which the termination of the pancreatic duct and its relation to the bile-duct is liable in the human subject, arranged in their order of frequency.

A. The normal arrangement, showing *a*, the bile-duct, and *b*, the pancreatic, terminating by one orifice.

B. Showing the separate termination of *c*, the accessory duct from the head, or lesser pancreas.

C. The main duct, *b*, terminating by an orifice distinct from the choledoch.

D. Two parallel and equal ducts *b*, *c*, are here seen joining the bile-duct at its orifice. This is a case of "double pancreatic duct."

Meckel, in the early fœtus, so that this irregularity is essentially nothing but an extension of a fœtal condition into adult life. When this duplicity of orifice exists, the separate duct from the head of the pancreas has its own little papilla, proportionately smaller than the normal one, and separated from it about $\frac{3}{4}$ths of an inch or an inch. It is usually lower down, though sometimes higher up, than the main orifice. It has been observed by Cruveilhier, that when there is one duct opening by a distinct orifice appropriated to itself alone, there is always another opening into the duodenum in the normal way in common with the ductus choledochus. According to other authorities*, however, the pancreatic duct and the bile duct will sometimes open on the mucous membrane of the duodenum by two entirely distinct orifices, when the former is single and there is no secondary one, as seen in *fig.* 55. C. Occasionally the pancreatic duct is double throughout its whole length, the two running side by side and communicating, just before

* Sœmmerring, Corp. Human. Fabrica.

their junction, with the ductus choledochus, as shown in *fig.* 55. D. Sœmmerring asserts that there are sometimes three ducts distinct throughout and opening separately. All the varieties of method of termination of the pancreatic duct have been collected and analysed by Tiedemann*; and he has come to the interesting conclusion that they all have their analogues in the different arrangements found in the various species of the lower animals.

The method of termination of the pancreatic duct, and its relation to the ductus choledochus, is rather curious. The duct, unlike the ducts of the salivary glands, which have a long course after leaving the gland before they terminate, passes at once from the gland to the intestine at a point where the former is closely applied to the latter, so that it is quite covered up and has no peritoneal investment. At this situation it comes into contact, at an acute angle, with the ductus choledochus, which has descended to this point either in a groove of the pancreas, between it and the intestine, or in a complete channel through the gland substance. The pancreatic is placed to the left of the choledoch duct; and, maintaining this relation, the two perforate obliquely the duodenum about the middle of its second portion and at the left side of its posterior wall.

Side by side they perforate in succession the muscular, the fibrous, and the mucous coats, which they elevate into a ridge when injected or when a probe is passed into them, and after an oblique course of about eight lines, they open into the bottom of a little papilla situated in a transverse fold near the junction of the middle with the third portion of the duodenum.† In their transit through the walls of the intestine they are separated by a valve-like process, composed of the tissues that constitute their walls, which gradually gets thinner and thinner till it terminates at the base of the little olive-shaped ampulla about two lines in depth, into which the cavity of the papilla is dilated; and since the mucous membrane lining this ampulla is of the same structure as that lining the intestine, and unlike that lining the ducts, these latter must be said to open by two distinct orifices at the base of the papilla, and not by one at its apex, as is usually described; in fact the lining membrane of the cavity of the papilla is part of the general mucous surface of the

* Sur les différences que le canal excréteur du pancréas présente dans l'homme et dans les mammifères. Journal Compl. des Sciences Médicales, tom. iv. p. 370.

† The point of immergence of the pancreatic duct is variously stated by various authors. *Sœmmerring* gives it as from three to twelve fingers breadth below the pylorus; *Meckel*, from three to four inches, but possibly amounting to ten; *Quain*, three to four inches; *Cruveilhier*, at the lower part of the second portion of the duodenum; *De Graaf*, quatuor digitis transversis sub pyloro; *Gavard*, five fingers breadth from the pylorus; and so on. That given in the text, which coincides with Cruveilhier, is the normal one; the extremes are very exceptional.

duodenum.* Towards its orifice the duct more or less enlarges itself; but at its very aperture, on the contrary, it undergoes a contraction. The appearance of a valve guarding the orifice depends merely on the partition which separates its mouth from that of the choledoch duct. Occasionally near the orifice, occasionally higher up, there is a valve-like process projecting from its inner surface ; but this is not constant either in its situation or its existence.

From the narrowness of the duodenal orifice of the pancreatic duct, from the movable and yielding nature of the eminence upon which it opens, and from the oblique course of the duct through the walls of the duodenum, it follows that the pancreatic fluid and the bile may pass freely *into* the duodenum, but cannot regurgitate from it into the ducts. "On this subject," says Cruveilhier†, "I have made several experiments. I have forcibly injected both water and air into the duodenum, included between two ligatures, but nothing escaped; on the other hand, I have injected the same fluids from the duct into the duodenum, which I was thus able to distend at pleasure. But then, on compressing the bowel with great force, I have never been able to cause the slightest reflux into the ducts." The spur-like process formed by the lining membrane reflected upon itself at the junction of the ductus choledochus and the pancreatic duct, extending down to the duodenal orifice, does not prevent the fluid of one canal from passing into the other. Thus the pancreatic fluid might regurgitate into the ductus choledochus, and, on the other hand, the bile might enter the pancreatic duct, if these canals were not habitually full. Moreover, this spur-shaped process between the two canals cannot arrest the flow either of the bile or pancreatic fluid, by being applied to the orifice of the one or the other duct.

Fig. 56. is a diagrammatic representation of the manner in which the ducts traverse the walls of the duodenum and terminate in the papilla, and of their relation to one another, and to the coats of the intestine.

Vessels.—The *arteries* of the pancreas, which, for the size of the gland, are large and numerous, are, like those of other conglomerate glands, contributed from many sources, and are derived from the branches of the cœliac axis, and from the superior mesenteric. The principal are the pancreatico-duodenalis of the hepatic and the pancreatic branches of the splenic artery,—one of which, the *pancreatica magna*, sometimes runs nearly the whole length of the gland, accompanying the duct from left to right. The branches from the

Fig. 56.

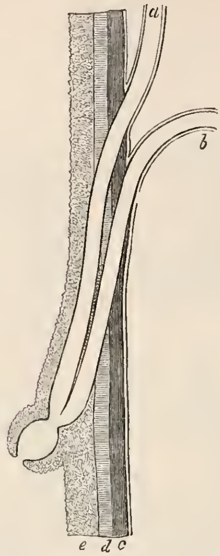


Diagram of the normal method of termination of the pancreatic and bile-ducts in the human subject, showing their oblique transit through the successive elements of the wall of the intestine, their gradual approximation to one another, their final union at the base of the ampulla or cavity of the papilla, and the spur-like process separating them.

a is the bile-duct; *b*, the pancreatic; *c*, *d*, and *e*, the muscular and mucous coats of the intestine.

superior mesenteric are mostly derived from that small twig which, given off just at the lower border of the pancreas, anastomoses with the pancreatico-duodenalis. The *veins* empty themselves into the superior mesenteric and splenic.

The *lymphatic vessels* have not, that I know of, been demonstrated, nor have I been able to detect them myself: they are supposed to enter the lumbar glands in the neighbourhood.

The *nerves* are derived from the solar plexus, and enter the gland at different parts, accompanying the branches from the arteries of the cœliac axis.

II. Microscopical Anatomy.

Gland substance.—The subject of the microscopical anatomy of the pancreas is one of great difficulty, and, until I came to examine it for myself, I had no idea how great. The delicacy and tenuity of the structures, even when seen most advantageously; the destruction of all their natural relations, and consequent impairment of the value of observations by cutting, tearing, or compression; the rapid change that takes place in the microscopical elements themselves, in whatever medium they are placed for examination, by deliquescence, solution, or endosmosis; the conflicting character of different appearances; and the discrepancy of many of them with the interpretations

* Sœmmerring considers the *apposition* of the two ducts in the wall of the intestine a *junction*, and the partition between them merely a valve: indeed, it is to that portion of the bile duct, so joined by the pancreatic, that he restricts the appellation *ductus choledochus*. "*Ductus choledochus, id est ductus hepaticus, cysticus, et pancreaticus in unum conflati.*" (Corp. Hum. Fab.) A definition as unphysiological as it is inconsistent with critical anatomy.

† Descriptive Anatomy.

given by the most trustworthy authorities, all conspire to invest the practical investigation of the subject with an amount of difficulty and doubt greater, I think, than that which would beset almost any other path of microscopical research. And I may add to this, what would naturally be its accompaniment, a deficiency on the part of the authors that I have consulted, in that very kind of information that the practical difficulties of original research make one crave in others. The only observations on which I think reliance is to be placed for the solution of the difficulties that the examination of a structure so involved and delicate as the one under consideration presents, are observations made with the microscope on the parts, fresh, *in situ*, unaffected by re-agents, and undisturbed by such manipulation as shall interfere with the normal relations of their minute anatomy; and such observations I cannot find. Müller's descriptions and drawings on this subject, in his admirable monograph, "De Glandularum Secernentium Structura Penitiori," are either taken from the parts unmagnified, or magnified with such low powers as make them valueless for the solution of the special difficulties of the case. The same observation applies to the accounts of the minute structure of the pancreas contained in the ordinary works on descriptive anatomy, from their being descriptions of the minute structure as seen by the naked eye, or as made out by a coarse kind of disintegration, or by mercurial injections.

The most satisfactory microscopical examinations of the pancreas may be made, I think, from those of the *Rodents*; for in them the gland being spread out in its proper mesentery in an arborescent or seaweed-like form, it is in some parts so thin as to transmit sufficient light for its examination without any compression or dissection whatever; indeed, along the edges and in some of the smallest lobules, the ultimate follicles are distributed in a single layer only. This arrangement makes a careful and satisfactory scrutiny much easier; and I shall, therefore, in this part of my paper, draw principally from the appearances of the gland in these animals, as the rat, rabbit, mouse; at the same time the close approximation in ultimate structure to the human pancreas will make my observations apply as well to the gland in man as in these lower mammalia.

On putting a minute lobule of the pancreas of a rat or mouse under the microscope, we see a number of follicles grouped together, of various forms and sizes, constituting, by their grouping, the acini of the gland, or ultimate granules visible to the naked eye; and when the acinus is constituted by a small number of follicles, and isolated, the whole of it may be brought under the field of the microscope at once (as in *fig.* 57.). These follicles are formed by the involution of the *limitary membrane* of the gland, and they contain the *secreting epithelium*, and within that (at least under some circumstances) a *central cavity*. These elements of the follicle — the basement membrane, the epithelium, and the cavity — I shall consider in succession.

Fig. 57.

Minute lobule or acinus of the pancreas of a Mouse, showing the two forms or stages of the epithelium, and the varied forms and sizes of the ultimate follicles (magnified 180 *diameters).*

a. The basement or limitary membrane.—It is to the modification and arrangement of this fundamental tissue that the pancreas (in common with all other glands, either follicular or tubular, simple or compound) owes its shape and appearance as a conglomerate gland, and its position in the gland series as a "compound gland with canals of the ramified type having follicular extremities."* From this membrane, as from a starting-point, the distribution and anatomy of all the other elements of the gland structure proceed. The branched character of the ducts, the particular manner in which the follicles are grouped, the racemose or panniculated character of their clusters, the isolation of the epithelium within them, the amount and arrangement of the areolar tissue without them, and the form of the capillary network, all result from the particular way in which this basement membrane is laid down. To this simple truth anatomists have been a long time in coming. Malpighi first, in 1665, announced the fact that the compound glands were mere multiplications or repetitions of the simple ones, and that all glands consisted of tubes with blind dilated or undilated extremities, which received the secretion from the blood and poured it into the excretory duct. This view, after having some doubt thrown upon it by the researches of Ruysch and the experiments of Haller, has been entirely confirmed and greatly elaborated by the labours of Müller, who, in his great work on the inti-

* Müller, Physiol. by Baly, vol. i. p. 444.

mate structure of glands, has contributed more than any other author to our knowledge of this particular section of general anatomy.

In the human pancreas the follicles are so closely packed that their individual shape cannot well be seen; but in the rodents the arborescent arrangement of the gland exhibits them well; and they are seen, when isolated, to be ovoidal or nearly spherical*, although, in the central part of the lobule, they become variously polygonal from mutual compression. The outline, however, even where they are not compressed, is not that of smooth spherules, but presents slight convexities corresponding to the epithelium within them; but the endosmosis of water, by detaching the epithelium from the basement membrane, and at the same time distending the follicle, causes these convexities to disappear. There is great difference in the size of the follicles, some being as much as $\frac{1}{200}$th of an inch in diameter, some as small as $\frac{1}{800}$th; and the extremes in size will often be contiguous, a very small one packed among many large. The average size of a pancreatic follicle is about $\frac{1}{500}$th of an inch. The number of follicles in a single group varies still more, being from half a dozen to a hundred or even more. In the rodents these groups are often entirely separate from one another on every side; but in most of the mammalia their isolation is not so complete, and they are more or less massed and fused together.

Fig. 58.

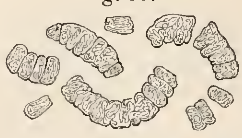
Isolated cells of mature secreting epithelium from the pancreas of the Rat, showing their opaque granular contents. (Magnified 400 *diameters.)*

β. The epithelium is of the glandular type, spheroidal or polygonal in shape, varying in diameter from $\frac{1}{1500}$th to $\frac{1}{2000}$th of an inch, and presenting two distinct appearances, indicating, I think, two stages of development — an early stage, and one of more complete maturity. The cells of the early stage are smaller, more spherical, homogeneous in structure, and most abundant at the peripheræ of the follicles or in immediate contact with the basement membrane. The more advanced cells are larger, of more varied shape, full of granular contents, and loosely aggregated towards the centre of each follicle. I consider the form first described to be the early stage because the cells are so small, are in contact with or near the cell-generating surface, and are free from secretion contents. The others, I imagine to be the more advanced stage, from their greater size, their loose and unattached appearance, the similarity of their granular contents to that of the secretion when free, and the want of definiteness of outline in many of them, which seem dissolving in their own contents, the cell-wall having disappeared, and the cluster of contained granules merely marking its situation. (See *fig.* 57.) In neither of the stages can I detect nuclei. From the great opacity of the more advanced cells, and their grouping towards the centre of the follicle, they give a portion of pancreas, viewed with a low power, a mottled appearance, a dark spot marking the centre of each follicle, and the number of dark spots showing the number of follicles, which, in some parts, from their close packing, could not be otherwise counted

When the follicles are ruptured, the epithelium escapes, and the two forms may be seen floating freely about. *Fig.* 58. represents some of the more advanced cells; they are magnified 400 diameters, and are seen to be filled with the particular granular matter which imparts to them their darkness and opacity, and which differs only from the free granular matter floating about in the secretion in being localized and confined by the vesicular envelope of the cell. What might be called the granular or molecular base of the pancreatic fluid, is evidently the contents of these mature cells, liberated by the rupture or solution of the cell-wall.

The cells that have attained this appearance, although they may be grouped together, as seen in *fig.*, 57. are never adherent to one another. The less advanced cells, however

Fig. 59.



Epithelium liberated by rupture of the follicles, showing the method of detachment, and the mutual lateral adhesion, of the cells. From the Mouse. (Magnified 200 *diameters.)*

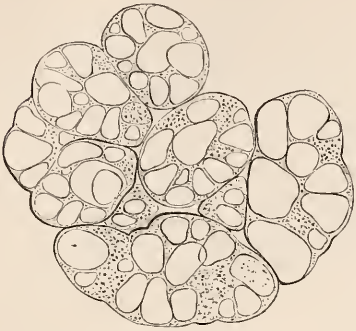
or those in contact with the membrane of the follicle, are often so closely adherent, that when they escape from their containing follicle they form little crescentic masses, as seen in *fig.* 59., the convexity coinciding with the follicle-membrane, the concavity with the central space, and the adherent surfaces of the cells presenting the appearance of radiating lines, passing from convexity to concavity at right angles to them: this close package of the epithelium gives it a columnar appearance; and, indeed, some of the little crescentic groups referred to closely resemble the scraps of sheaths of columnar epithelium shed from an intestinal villus during digestion.

Sometimes, instead of the follicles being filled with distinct epithelium cells, they appear to contain a number of variously-sized globules, of a smooth, homogeneous, and highly refracting appearance, surrounded by a medium of much less refracting power, and

* In Cruveilhier's Anatomy, p. 533. note, it is said that the ultimate follicles of the pancreas are cylindrical, while those of the salivary glands are slightly dilated. (?)

finely granular. These globules are of various shapes, according as they are isolated or com-

Fig. 60.



Appearance of homogeneous globules of various sizes and shapes, occasionally seen in the follicle of the pancreas. From the Rat. (*Magnified* 200 *diameters.*)

pressed by neighbouring ones. They range in size from $\frac{1}{1500}$ to $\frac{1}{400}$ of an inch, and are evidently not contained in any cell-membrane. (See *fig.* 60.) The appearance, in my opinion, results from a spontaneous solution of the epithelium in the follicles, and a separation of the different elements of the secretion; but what are the particular circumstances that determine it I do not know; the longer the object is kept under the microscope, the more marked is the appearance, and the larger the globules, from their running one into the other: it is possible that endosmosis may have something to do with it, for I do not remember ever to have seen the appearance in specimens promptly examined immediately after death.*

γ. Occasionally there is an appearance of a central cavity in each follicle, the epithelium lining it in a single columnar-looking layer, and leaving a central space unoccupied. The central space thus left is very small, not exceeding in diameter that of the thickness of the epithelial layer lining the follicle; it is only now and then that this appearance can be detected, and even then it requires careful focussing to see it satisfactorily: it may either arise from the epithelium being shed in successive generations of layers,—one passing from the follicle as the succeeding crop is produced,—or it may be explained by the mere liquefaction of the central and older cells, which, escaping in a fluid form from the follicle, leave the peripheral cells with a definite and even surface. At any rate, it is a rare thing to see the appearance clearly, and when it is visible, it requires accurate focussing for its satisfactory display; for if either the nearer or more distant surface of the follicle is in focus instead of the centre, all appearance of cavity vanishes, and the follicle seems to be full of epithelium. Perhaps it is in part owing to this, and in part to the fact that the condition accompanies a particular and transitory stage of the secretion, that it is

Fig. 61.

A group of follicles from the pancreas of a Rat, viewed so as to bring their central cavity into focus. (*Magnified* 150 *diameters.*)

not more frequently visible. I have represented it in *fig.* 61., as seen in a group of follicles from the pancreas of a rat: it displays the proportional thickness of the central cavity and the epithelial lining, and shows one or two follicles, where, from being out of focus, the cavity is not visible and the follicle appears solid throughout. It was sketched immediately after death.

Duct.—The duct of the pancreas, like that of other conglomerate glands, consists of three coats: a middle, elastic, dense, fibrous, and white; an external, loose, and areolar; and an internal epithelial. Between the middle and internal there is probably a basement membrane, described, indeed, by some authors, but which I have been unable to detect.

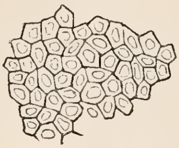
The middle coat consists of a firm, dense, and matted stratum of fibrous tissue, mainly longitudinal in direction, but closely interwoven and netted together, very much resembling white fibrous tissue in appearance, but evidently not consisting of this entirely, as the striation is not removed by acetic acid. A certain amount of clarification, however, is produced by adding the acid, and the fibres that remain visible afterwards appear to consist of a particular form of yellow fibrous tissue, extremely fine, so as to lose the characteristic appearance of double outline and even calibre. These fibres are exclusively longitudinal and parallel, except towards the outer surface of the duct where they interlace. Besides these, acetic acid displays, irregularly and sparingly scattered, some transverse and some longitudinal, the nuclei of some unstriped muscular fibres. These fibres I have never been able to isolate or see satisfactorily, for the density and opacity of the fibrous tissue previous to the addition of acetic acid renders them invisible: they lie near the inner surface, and, from the paucity of the nuclei, must be very few.

The external coat is merely the loose areolar web which connects the duct to the

* Since writing the above, I have had satisfactory evidence that the appearance is owing to endosmosis. I have seen the globules form under the microscope from their first trace to their attainment of a size equal to that shown in the figure. Sometimes the endosmotic current is so strong as to cause visible movement in the contents of the follicles; the globules are the endosmosed fluid, the intervening material the granular contents of the follicle; in fact, the secretion. I have thought it worth while to retain the figure and description, as it is an appearance that might very easily give rise to error.

gland substance, and is continuous with that which pervades the whole gland: it differs not, therefore, from that which has been already described.

Fig. 62.



Tesselated appearance of columnar epithelium lining the pancreatic duct. (*Magnified* 200 *diameters.*)

The epithelium is columnar, arranged apparently in a single stratum, and presenting a beautiful honeycomb appearance of closely-packed hexagons and pentagons, when looked at on its free surface. Further up, however, near the extremities of the ultimate ducts, the epithelium changes its character, and becomes more globular, as is shown in *fig.* 63, which represents a portion of the epithelial lining of a duct, about $\frac{1}{400}$ of an inch diameter, from the human subject. A certain approximation is here seen to the form of secreting epithelium, with which, however, it strongly contrasts in its clearness and freedom from granular contents.

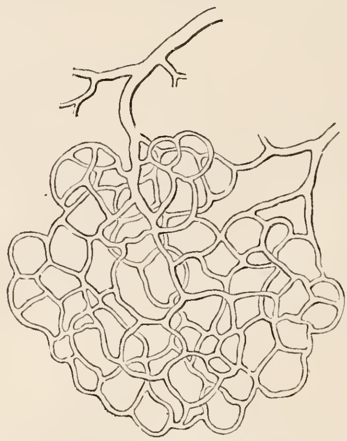
Fig. 63.

Portion of epithelium lining a small duct $\frac{1}{400}$*th of an inch in diameter. From a Rabbit.* (*Magnified* 300 *diameters.*)

There is every probability of the existence of a basement membrane here as in other sub-epithelial situations, and it is probably continuous with that which alone constitutes the walls of the ultimate ducts: for the fibrous and muscular elements gradually diminish as the ducts get finer, until in the smallest that are seen all fibrous appearance has vanished, and a homogeneous membrane alone remains. According to Henle the homogeneous wall of the smallest ducts consists of fibres fused and run together in a plane; — a supposition that would imply the non-existence of this membrane in the larger ducts, where they are not so fused.

Capillaries. — The arrangement of the capillaries remarkably resembles that of fat. They form a close and pretty even-meshed net work, open on all sides, among the meshes of which the follicles lie, just as the vesicles do in the case of fat; so that the closeness of the plexus is a measure of the size of the follicles. Their general appearance is well seen in the accompanying figure (*fig.* 64.).

Fig. 64.



Arrangement of the capillaries of the pancreas. From a minute lobule of the pancreas of a young Rabbit. (*Magnified* 80 *diameters.*)

III. Comparative Anatomy.

Invertebrata. — Certain organs connected with the alimentary canal have in some of the higher invertebrata received the name of pancreas; but they have done so rather from their position and inferred function than from any certain evidence of their use, or from their anatomical structure. In *Gasteropoda* we find the first indications of the organ, and it presents in them the form of a single, long, blind, glandular sac, communicating with the beginning of the intestine; such a pancreas may be seen in the different species of Aplysia and Doris, Tritonia and Scyllæa.

Cephalopoda.—The Tetrabranchiate Cephalopods possess, attached to the upper part of the intestine, a laminated sac, which receives the canal into which the two main hepatic ducts unite, and which diverts the bile by a peculiar development of one of its laminæ, from flowing into the gizzard. Professor Owen considers that the follicular structure of this and the other folds of membrane sufficiently indicate its glandular character, and regards the entire laminated pouch as a more developed form of pancreas than the simple cæcum, which we have just described as representing that gland in some of the Gasteropods.

Vertebrata. — *Fishes.* — At the commencement of the intestinal canal, close to the pylorus, are found, in most osseous fishes, certain cæca or blind tubes, budding out from the wall of the canal, which from their position have received the name of *pyloric appendages*, and have been regarded by most anatomists as the analogue of the pancreas in higher animals. In their most simple form— that of a single, or two or three short buddings of the intestinal wall, not differing from it in the structures that form them, the analogy would hardly suggest itself, but by gradual steps we are conducted from this simple representative of the organ, through a series of forms of increasing complexity, to a structure bearing some analogy to a conglomerate gland, and at any rate deserving to be considered a special glandular appendage to the alimentary canal; the cæca becoming more and more numerous as we ascend in the scale, and the whole organ more and more concentrated. Thus in the Sandlance (*Ammodytes lancea*), and Polypterus there is but one pyloric cæcum; in most of the Labyrinthibranchs, in many species of Amphiprion, in the Angler (*Lophius piscatorius*), Turbot (*Pleuronectes maximus*), and Mormyrus there are two; in the Perch (*Perca fluviatilis*), the percoid Popes, the Asprodes and Diploprions, three; in the Miller's Thumb (*Cottus gobio*), and Father Lasher (*Cottus scorpius*), from four to nine; in the Gurnard (*Trigla*), from five to nine; in Scorpæna and Holocentrum, six and upwards; in the Pilchard (*Cupea pilcardus*), and Lump-fish (*Cyclopterus lumpus*), there are fifty, and upwards of fifty in the Tunny (*Scomber thynnus*); in the Cod (*Gadus morrhua*), there are upwards of 120: and in the Sturgeon (*Acipenser sturio*) and Paddle-fish they cannot be counted.* But the increased complexity, and divergence from the simple cæcal form, is not produced only by the greater number of the appendages. As they increase in number, they more and more coalesce at their bases, so that many cæca open by few orifices, and thus the character of the gland is gradually changed, becomes clustered and branched, and passes from the tubular to the racemose type. Thus, in the Pilchard, fifty tubes communicate with the intestine by thirty orifices; in the Lump-fish the same number by six; in the Tunny, by five; in the Sword-fish (*Xiphias gladius*), there are but two orifices; and in the Sturgeon, the whole mass of cæca, by continually uniting and re-uniting, come at last to empty themselves into a single tube, equivalent, in fact, to a short and wide pancreatic duct.

The reasons which have induced anatomists to regard this organ as the analogue of the pancreas are these.

* Owen's Lectures on Comparative Anatomy.

In the first place, the *situation*; it is placed at the pyloric extremity of the intestine; and besides this general similarity in situation, there is this special one, that the hepatic duct has the same relation to it as it has to the pancreas in higher animals. If there is but one orifice, as in the Sturgeon, the hepatic duct opens at its base; if many, at the base of one of them.

Secondly. If they were merely multiplications of surfaces to which food was to be exposed, we should find food getting into them; but this is never the case. I have not been able to detect any alimentary materials in even the largest of them; their function therefore must be that of pouring forth some special secretion.

Again, it is not the way, the particular method, in which surface is multiplied; that is done by modifications of the lining membrane of the intestine, the mucous structures, alone — by folds, villi, crypts — and not by extension of the whole intestinal wall, muscular and sub-mucous, as well.

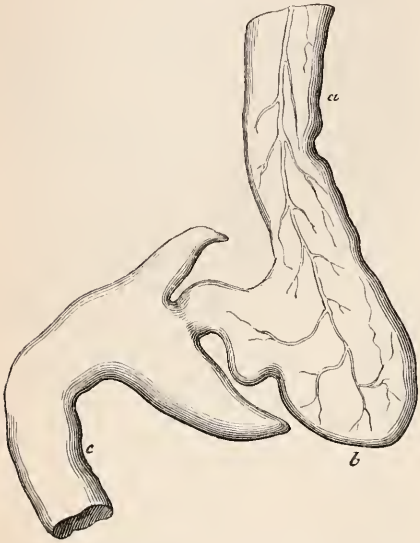
Lastly, the filling up of all the intervening stages from simple tube to conglomerate pancreas goes a great way to prove the essential identity of the extreme forms.

But what is very remarkable with regard to these appendages is their entire absence in many classes of fish. In all the Abdominal Malacopterygii, except the Salmonidæ and Clupeidæ, they are wanting; in most of the Labroids, Gabioids, Cyprinoids, and Lucioids, they are absent; in the Apodous Malacopterygii, in the Lophobranchs and Plectognats there is no trace of them; nor in the genera Antennarius, Malthæus, and Batrachus In some cases they appear to be wanting in consequence of their place being supplied by a more elaborate mucous surface, as in the highly developed stomach of the Anarrhichas, and the glandular palate and long intestine of the Carp (*Cyprinus*); in others, their absence seems to be but a part of a general simplicity of the alimentary apparatus, as, for instance, in the Dermopterous fish. In the Eel, where there are no cæca, the mucous membrane at the pylorus suddenly becomes thick, vascular, and spongy, and continues so for about an inch; and on pressure an abundant secretion may be squeezed out of its wall, of an appearance exactly identical with that found in the pyloric appendages where they are present.

It is difficult to seize on the law of their existence; we may, however, say that they are, for the most part, wanting in fish that live on vegetable substances, although there are many similarly circumstanced that are carnivorous and very voracious. Their development, or their relative size, their number and complication, are probably in proportion to the activity of digestion and rapidity of growth; the Salmonidæ, the Clypeidæ and Scomberidæ, seem to indicate this: in these last these pyloric cæca exhibit a remarkable complexity.

In the Turbot (*Pleuroneetcs maximus*) these cæca are seen in their most rudimentary form; they are two in number, ample, conical, and recurved, projecting back from the duodenum at its very commencement, so as to give it a barbed or arrow-head appearance, as seen in the drawing (*fig.* 65.). The stomach in this fish is very small, and the duodenum

Fig. 65.

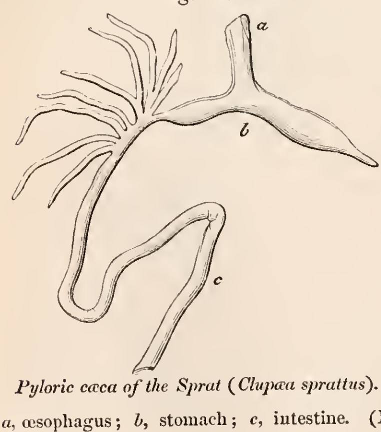


Pyloric cæca of the Turbot.

a, œsophagus; *b*, stomach; *c*, intestine. (Drawn one-third the natural diameter.)

very large, and the food probably passes into the intestine with but little delay. The cæca in this case must be considered an exception to the rule I have above laid down, that they are never filled with the contents of the alimentary canal; for in the specimen I examined they were completely stuffed with tæniæ, with which also the intestine was filled.

Fig. 66.



Pyloric cæca of the Sprat (*Clupæa sprattus*).

a, œsophagus; *b*, stomach; *c*, intestine. (Natural size.)

In the *Sprat*, the pyloric cæca are nine in number, long, slender, and simple (see *fig.* 66.): the upper five unite together at their bases, and open into the duodenum, close to the pylorus by one orifice; the last four open separately, each by its own orifice, in linear series along the duodenum.

In the *Gadidæ*, as in the *whiting* (*fig.* 67.), the cæca are arranged in the form of a ring,

Fig. 67.

Alimentary canal of the Whiting (*Merlangus vulgaris*), *showing the pile of cæca around the pylorus.* (*One half the natural diameter.*)

constituting a frill around the intestine, and consits of four bunches, each containing about thirty cæca. These unite and re-unite till they terminate, each bunch, in a single duct; so that there are finally four orifices, so placed as to fall on two converging sides of a triangle, of which the orifice of the hepatic duct would form the apex. As each bunch contains thirty cæca, there are a hundred and twenty

Fig. 68.

One of the four bunches of pyloric appendages of the Whiting, isolated; showing their union and reunion till at length they end in a single tube.

in all. The appearance of the frill of pyloric cæca is shown in fig. 67, and one of the bunches separate in fig. 68.

In the *Salmon* this apparatus of cæca is much more voluminous. It is not condensed around a particular portion of the intestine, but extends linearly, from close to the duodenum for a distance of about eight inches along the intestinal wall; each cæcum opens by its own separate orifice. There is no coalescence or fusion, so that on looking on the inside of the intestine there are seen as many orifices as cæca; they form a double row on each side, so that altogether there are four rows, and are arranged with the utmost regularity. The amount of secreting surface of these cæca must be very great; some of them are ten inches long, and as big round as a tobacco-pipe; they rapidly increase in length from the first three downwards, and the third from the stomach is generally the longest. They then gradually diminish, slightly in calibre, considerably in length, to those furthest down the intestine, which are about three inches long. Altogether the secreting surface of these cæca must considerably exceed that of the rest of the alimentary canal, and the whole apparatus, taken together, is next to the liver, by far the largest of the viscera. Each double row contains about thirty, so that altogether there are sixty cæca, and as the average length of each cæcum is $6\frac{1}{2}$ inches, the whole length of secreting surface must be 390 inches, or upwards of 32 feet.

Fig. 69.

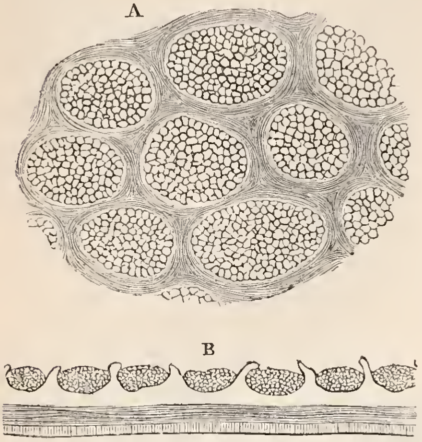
Portion of the alimentary canal of the Salmon (Salmo salar), showing one double row of cæcal appendages and the pyloric extremity of the other.

a, œsophagus; *b*, stomach; *c*, pylorus; *d*, small intestine; *e*, gall-duct. (One-third the natural diameter.)

In their internal ultimate structure these cæca exhibit considerable variety; in many the mucous surface is closely laminated; in some it is covered with flattened, fused villi with crypts thickly planted between their bases. In the Herring (*fig.* 70.) the structure is very peculiar: on looking vertically on the internal surface it is seen to be mapped out into hexagonal and pentagonal cells about $\frac{1}{150}$ of an inch in diameter, very evenly and geometrically arranged, and each filled with a mass of epithelium. The septa between them appear to consist of submucous fibrous tissue, and on making a section and looking at it laterally they are seen to project between the acervuli of epithelium, and rather beyond them, and to have no epithelial investment of themselves. The masses of epithelium are seen to be of a spheroidal form and very smooth outline, though I could not distinguish any basement membrane or capsule wall of which they might be supposed to be the contents, or any special structure determining their outline. I have thought this structure sufficiently peculiar to give a figure of it. A represents the appearance on looking down on the surface; B, a view of the wall in section, seen with a lower magnifying power.

Many anatomists deny the true pancreatic nature of these pyloric cæca, and assert that many fish possess, over and above them, a true glandular pancreas, analogous in structure to the pancreas of higher animals. Weber first described such an organ in the *carp*, as interlaced with the lobules of the liver, and, so to speak, confounded with them, but having a proper excretory canal opening into the intestine by the side of the cystic; he also thought that he had seen traces of a pancreatic duct in the *pike*. Much more recently Alessandrini described the same excreting duct, as also the volume and position of the pancreas, in the same fish. In the *Silurus glanis* MM. Brandt and Ratzebourg have taken for the pancreas a glandular body very like the liver in appearance, stretched as a layer between the folds of the gastro-hepatic omentum, enveloping the cystic canal and accompanying it as far as the intestine. These three examples of malacocopterygious fish have no pyloric cæca, and this glandular structure might be considered as replacing them; but Alessandrini has also described in the *sturgeon*, the walls of whose intestinal canal are particularly glandulous and in which the pancreatic cæca form an elaborate apparatus, a proper pancreas with an excretory duct opening into the intestine in the middle of a tubiform papilla about an inch from the pyloric orifice. In this last case Cuvier believed the body indicated as the pancreas to be a lobe of the liver. "The tubiform papilla," he says, "truly exists; indeed I have found two, besides that appertaining to the choledoch duct. In one of the examples it formed a sort of *cul-de-sac*; in the other the fibre which was introduced conducted to a canal which took a direction towards the liver. I have clearly seen an excretory duct in a very large silurus, piercing the intestine of the side of the choledoch; but that canal was, in my opinion, hepatic, for the glandular substance taken as the pancreas was evidently continuous with the right lobe of the liver, and formed, as it were, a middle lobe; its appearance was in other respects the same, except that its colour was rather clearer in consequence of its substance being less thick at that part. The duct discovered in the *pike* certainly exists, as far as my researches go; but that, again, is an hepatic canal, for I have not seen any body distinct from the liver from which it takes its origin, or which could be considered as a pancreas. The same must be said of the *carp*, where Meckel could discover neither a pancreas nor pancreatic duct, in spite of the indications of Weber." Still more recently Stannius has enumerated many fish in which a parenchymatous pancreas may be found; but the description added to his enumeration is so meagre and general that nothing can be verified upon it.

Fig. 70.



Mucus membrane of the interior of the pyloric cæcum of a Herring (*Clupæa harengus*).

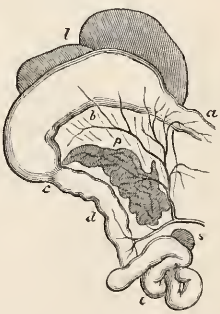
A, the surface seen vertically, showing the honeycomb appearance formed by the septa separating the masses of epithelium. (Magnified 150 diameters.)

B, a section vertical to the surface, showing the flattened spheroidal shape of the acuvuli of epithelium, and the amount of projection of the septa between them. (Magnified 60 diameters.)

Reptilia. — In the reptiles we make a great approach to the structure of the pancreas of higher animals both in general form and structural appearance. It exists in them all, and generally maintains that intimate relation to the end of the stomach and commencement of the intestine which we see so constant in birds and mammalia.

In the *Batrachia*, the pancreas is situated in a proper mesentery or meso-gastrium of its own, extending between the lesser curvatur of the stomach and the duodenum, and, according to Cuvier, is more developed in *terrestrial* batrachians than in *aquatic*, in those that take their nourishment out of the water than in those that hunt and seize it in the water. In the *Frog* (*fig.* 71.) the pancreas is shaped not unlike that of the human subject, but its broad end is in the opposite position; it is about three quarters of an inch long, weighs ·27 of a grain, and is of a yellowish white colour and soft consistence; it is in close apposition with the duodenum all the way along. From near the large end it sends up a process clothing and concealing the gall duct as far as the gall bladder, the neck of which it invests. The whole of the gall duct, till the point of its immergence into the intestine, is thus concealed in the substance of the gland, and it might at first sight be mistaken for the pancreatic duct; but, by carefully nicking it and introducing a fine hair, the hair may be passed up to the liver. The most careful dissection could not reveal a proper duct; probably small ducts from different

Fig. 71.



Pancreas of the Frog, shown by throwing up the stomach, and exhibiting the under surface of the mesogastrium.

a, œsophagus; *b*, stomach; *c*, pylorus; *d*, duodenum; *e*, small intestines; *l*, liver; *p*, pancreas; *s*, spleen. (Natural size.)

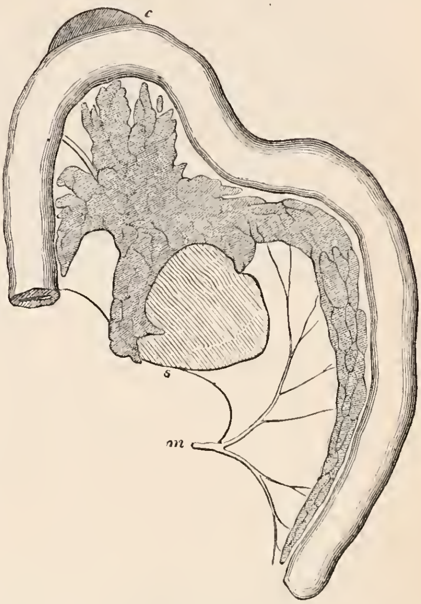
parts of the gland open into the biliary duct as it passes through. The organ maintains the same relations in the *Toad;* in the *common toad* it is yellow, straight, and elongated. In the *Tritons* it is perceived with difficulty; Cuvier describes it as appearing like a semi-transparent riband sending one bifurcation to the spleen, and another to the duodenum at the point of insertion of the biliary canals. In the *Siren* it resembles in miniature, as far as external appearance goes, the pancreas of the sturgeon, and joins the intestine by many parallel canals considerably in front of the cystic.

In *Ophidian* reptiles, the pancreas varies greatly both in volume and form; sometimes it is elongated, often globular and pyramidal, sometimes divided into two triangular lobes, and this variety of form obtains even in congeneric species; thus, in the *Cæcilia albiventris* it is thick, and pyramidal, and in the *Cæcilia interrupta, lumbricoïdes*, and *dentata*, it is straight, elongated and slightly forked. It is always placed to the right of the commencement of the intestinal canal and head of the stomach. Its substance is red with a tint of yellow, and soft, more rarely firm and consistent, and often divided into distinct lobes. In this respect it does not at all resemble the salivary glands of these animals, but those only of mammifera. Its intimate union with the spleen is very remarkable in the *true serpents*, whilst in the *genus Anguis* and *Cæcilia* the contact and adhesion at this point does not exist.

In the *Saurian* reptilia the pancreas is often applied against the pyloric portion of the stomach and the commencement of the duodenum; or it may be said to have two branches parallel to the stomachal sac, one of which accompanies the biliary canal, and the other adheres to the spleen, and these reuniting terminate at a point more or less approaching the pylorus; it is almost always contiguous to the choledoch canal, which often traverses it before arriving at the intestine. According to Cuvier, its volume is greater in saurians living on vegetable food; and its smallness in those that are carnivorous he believes to be compensated, as in fish, by the agency of the mucous and intestinal secretion of the abundant glandular apparatus with which their alimentary canal is furnished. In the *Lacertidæ*, and *Iguanidæ*, the pancreas is very much developed.

Chelonia. "In many respects," says Cuvier, "the animals of this order are in the same conditions as birds. The jaws are similarly armed, the salivary glands are but little developed, and as the volume and importance of the pancreas in birds has appeared to us to be in inverse ratio to the means of mastication and insalivation, we might antecedently conclude that the chelonia would also possess a considerable pancreas." At the same time he adds, that the superior masticatory power of the horny jaws of the chelonia over the bills of birds, and their taking their prey generally in the water, considerably impairs the closeness of the analogy. In the common *turtle*, the pancreas (*fig.* 72.) firmly adheres to and embraces the spleen; from that point it radiates towards the duodenum, being thick, amassed, and irregularly arborescent above and to the right, and continued in a long and tapering tail to the left: it is closely attached to the duodenum along its whole extent, a distance of about fifteen inches. The duct, nearly as large as in the human subject, passes to the right, and enters obliquely the choledoch duct, as that canal is perforating the thick intestinal wall, in a way very analogous to that already described in the human subject. The gland substance has a very peculiar appearance; it is dense, opaque, nearly white, and along its edges the lobules are scattered in the clear gelatinous-looking cellular tissue in which the gland is embedded, and appear to be quite distinct from each other; but on dissecting them out from this gelatinous bed, they are seen to be attached by little pedicles—in some of gland substance, in some apparently merely of the duct of the lobule and its vessels — to the rest of the gland. It is the most arborescent and ramified pancreas I have seen, next to the *rodents*, but not so flattened, nor spread out so much in one plane. When looked at as an opaque object with a low power (one inch focal distance), the mapping out of the follicles is very prettily seen; but the same circumstance that lends them their

Fig. 72.



Pancreas of the Turtle, with the duodenal curvature thrown up, showing its loose and branched character, its embrace of the spleen, its long caudate process accompanying the duodenum, and its duct entering the intestine higher up.

s, spleen; *m*, branch of superior mesenteric artery; *c*, gall-bladder.

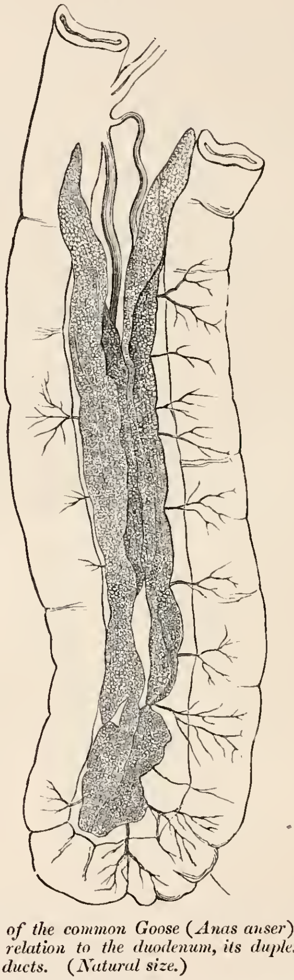
white opacity, — their fulness, that is, of a densely opaque granular material—prevents their being seen to advantage as transparent objects, or with a high power; they are so opaque that nothing of their structure can be distinguished. When ruptured by pressure, their contents escape, and are seen to consist of two very distinct materials; one, the aforesaid fine granular matter; the other of clear, spherical, uninuclear cells of about $\frac{1}{1000}$ of an inch diameter. One would imagine antecedently that these would hold the relation to each other of secreting epithelium and elaborated secretion; but the cells are so clear, so free from granular contents, and there is such a complete absence of any intermediate appearance, that I am at a loss in what way to interpret them.* The duct opens by a single orifice, and in a way admirably adapted for preventing the regress of the secretion, or the entry of the contents of the alimentary canal into it. If the aperture in the centre of the papilla by which the bile duct terminates is opened up, it is found to lead into a lacuna, or *cul-de-sac*, of about half an inch in length, embedded obliquely in the walls of the intestine. At the bottom of this lacuna is a second papilla, the real termination of the pancreatic duct. Now, if the movableness of the external papilla and the smallness of its aperture were not sufficient to prevent the ingress of the contents of the alimentary canal, yet the very force that might drive in some of these contents through the outer papilla, would press the walls of the lacuna firmly against the orifice of the internal one, and so effectually close it; nothing could be more efficient than this form of double orifice.

The duct in all reptilia always enters the duodenum, generally separate, sometimes in conjunction with the choledoch, and is almost always simple.

Aves. The pancreas of birds is proportionally larger than in any other animals; and when we remember their deficiency in salivary apparatus, its great development would at once suggest a function, in some degree, at least, supplementary to those organs. Another circumstance peculiar to birds and indicative of the importance of the part that the gland plays, is that the ducts are generally many, two and three, and that they open by separate orifices, and often at a considerable distance from one another; so that the secretion may be poured forth on different and widely separate portions of the alimentary contents at one and the same time, a circumstance that must greatly increase and expedite its action.

Birds, we know, seize and swallow their food generally without any mastication, and therefore it is not until it gets to the gizzard that it is subjected to any mechanical force capable of breaking it up. This, therefore, takes place immediately before entering the duodenum, and this throws the function of mastication close down to the pancreas, so that from its situation, as well as in other respects, it should have an insalivating function. It is always enclosed between the two arms of the duodenal flexure (*fig.* 73.); the duodenal portion of the gland being, so to speak' alone developed. It is retained in this position by the gastro-hepatic and gastro-colic omenta, which sometimes simply attach it to the border of the intestine, and sometimes allow it to be free and floating. There is considerable variety in its shape, but it is always more or less elongated and slender: sometimes it is undivided and single, in some species deeply cleft, in others consisting of two portions, or a double pancreas, quite distinct, each having its own duct; sometimes it is divided into three as in the pigeon. But

Fig. 73.



Pancreas of the common Goose (Anas anser), showing its relation to the duodenum, its duplex form, and its ducts. (Natural size.)

* The follicles appear to contain only the granular material, and in a minute duct I saw a number of the nucleated cells. It is possible that they may be a form of epithelium restricted to the terminal ducts, by whose rupture and compression they escaped, as the granular matter did from the follicles.

these arrangements are liable to considerable variety, and perfectly independent of the intimate structure and function of the gland, for in different individuals of the same species, the arrangement of the ducts is generally the same, however the segmentation of the gland may vary. The gland substance is firm, much more dense than in other orders, and not divided so distinctly into lobes and lobules: it has a finely granular and mottled appearance, in colour pink, or a little yellowish, or brownish. The pancreas seldom communicates with the intestine in birds by a single canal, the ducts are generally either two or three in number, and each continues independent and separate to its orifice. They do not communicate either with one another or with the biliary canal: although, however, exceptions are very rare, Cuvier has met with an instance in the *stork*, in which the single pancreatic and hepatic ducts united and opened by a common orifice.

The following table, altered from Cuvier, shows the number of the pancreatic ducts in several orders of birds, and their relative situation with regard to the hepatic and cystic ducts; it also shows the relation of these last to one another. That canal which is first indicated has its insertion the nearest to the pylorus; P. stands for *pancreatic*, H. for *hepatic*, and C. for *cystic*.

We see from this table, that, as a rule, the

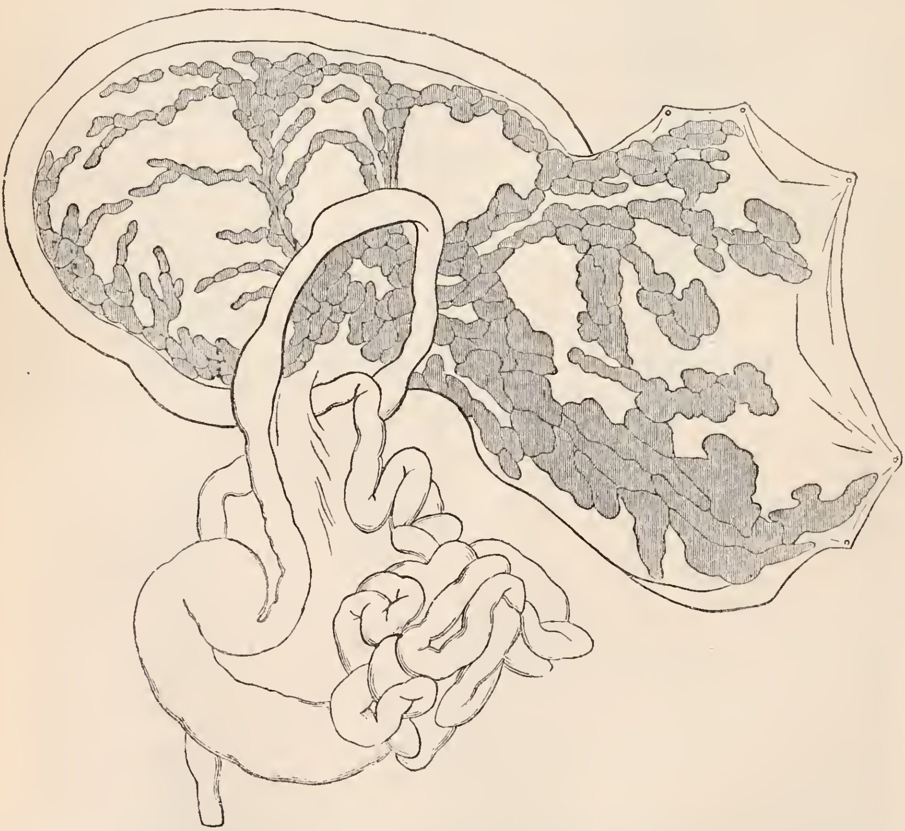
I. Raptores.						
Brown Vulture -	1 P.	H.	2 P.	3 P.	C.	Duv.
Common Eagle -	H.	P	C.			Duv.
Golden Eagle -	H.	C.	P.			Cuvier.
Aquila Ossifraga -	1 P.	H.	2 P.	3 P.	C.	Perrault.
Owl - - -	1 P.	2 P.	3 P.	H.	C.	Cuvier.
II. Insessores.						
Night-jar - -	H.	P.	C.			Cuvier.
Crow - - -	1P.	2 P.	H.	C.	3 P.	Cuvier.
III. Scansores.						
Picus (*Genus*) -	1 P.	2 P.	3 P.		C.	Meckel.
Green Woodpecker	1 P.	2 P.	3 P.	C.	H.	Cuvier.
Parrot - -	1 H.	1 P.	2 P.	2 H.		Cuvier.
Blue Macaw -	1 H.	{2 H. P.}				Duv.
IV. Rasores.						
Crax (*Genus*) -	1 P.	2 P.	1 H.	2 H.		Perrault.
Crax Globicera -	1 P.	2 P.	C.	1 H.	2 H.	Perrault.
Common Cock -	1 P.	2 P.	3 P.	H.	C.	Duv.
Quail - - -	P.	H.	C.			Cuvier.
Pigeon - -	1 H.	1 P.	2 P.	2 H.		Duv.
Bustard - -	1 P.	2 P.	H.	C.		Perrault.
Ib. - - -	1 P.	2 P.	3 P.	H.	C.	Meckel.
Cassary - -	P.	C.	H.			Perrault.
Rhea Americana -	H.	P.	C.			Meckel.
Ostrich - -	H.	P.				Perrault.
V. Grallatores.						
Stork - -	P.	H.	C.			Cuvier.
Bittern - -	H.	P.	C.			Duv.
Heron - -	1 P.	H.	2 P.	3 P.	C.	Cuvier.
Grus pavonica -	1 P.	H.	2 P.	C.		Duv.
Grus virgo -	1 P.	2 P.	H.	C.		Perrault.
Curlew - -				H.	C.	Duv.
Ib. - - -	1 P.	2 P.	H.	C.		Cuvier.
Gold-headed trumpeter - -	1 P.	H.	C.			Duv.
Flamingo - -	1 P.	2 P.	3 P.	C.	H.	Cuvier.
Ib. - - -	1 P.	C.	H.			Meckel.
Parra Jacana -	H.	1 P.	2 P.			Cuvier.
VI. Natatores.						
Grebe - -	1 P.	2 P.	3 P.	H.	C.	Meckel.
Great Diver -	C.	H.	P.			Duv.
Apterodytes -	1 P.	2 P.	H.	3 P.		Cuvier.
Gull - - -	1 P.	2 P.	H.	1 C.	2 C.	Meckel.
Petrel - -	1 P.	2 P.	H.	C.	3 P.	Meckel.
Swan - -	1 P.	2 P.	H.	C.		Cuvier.
Duck - -	1 P.	2 P.	H.	C.		Duv.

pancreatic secretion is the first poured into the intestines, and the cystic bile the last: and always when there are three pancreatic ducts, the secretion reaches the intestine early by one of them, and the others have their openings close to the bile ducts, either before or between them. It is not safe, however, to draw any physiological conclusions from these relative positions, even supposing them to be constant; for the ducts are so close to one another, that the mixture of the fluids must take place immediately, and their action on the food be simultaneous. In one instance, however, this is not the case; in the ostrich the bile duct opens close to the pylorus, while the pancreatic is three feet removed from it; this is the greatest separation of the two ducts of any with which I am acquainted in the animal kingdom. It would present, if ostriches were commoner birds, great facilities for experiment, and implies an action in both the secretions entirely independent and autocratic.

Mammalia.—The chief differences between the pancreas in other mammalia and man relate merely to its colour, its consistence, its more or less marked division into lobes, its form, its volume, its union into a single mass, or its separation into two distinct parts, lastly, its position and relations with different portions of the peritoneum. Its form is generally more or less that of a narrow band, divisible into two portions; one, the *duodenal*, following the curvature of the duodenum, and placed vertically or obliquely; the other, *gastro-splenic*, extending transversely, and therefore opposite the other, from the duodenum to the spleen, against which it always abuts; the latter is always developed, the former is often inconsiderable or suppressed, and must be considered merely as an accessory portion. The various forms and arrangements of the pancreas do not appear to have anything to do with its essential structure or function, or the particular exigencies of the animal; they seem to depend entirely on the relations of the neighbouring organs, the presence or absence of an abundant mesentery, the free movement of the duodenum, &c., and to be influenced by considerations of package.

In the *Ourang* the form very much resembles that of man; in most other *Quadrumana*

Fig. 74.



Pancreas of the Rat (natural size), shown by throwing up the duodenum, together with its proper mesentery, and the free process of peritoneum extending thence to the left, in which the gland ramifies. Its arborescent form and great extent are well shown.

it is irregular. In the *Carnivora* it is always large in proportion to the size of the animal*, both the duodenal and gastro-splenic portions being highly developed. In the *ox*, from the distinctness of the two portions, the organ has a bilobed appearance. In the *horse*, from the gastro-splenic portion being double, it has a trilobed form. But the most remarkable pancreas is that of the *Rodents;* it is spread out in an arborescent manner, in an extensive mesentery that imparts free movement to the long duodenum, and extends towards the left in a sort of omentum, which underlays the stomach. (*Fig.* 74.) Confined thus between the two layers of a mesentery, the ramified lobes of the pancreas lie all in one plane. Although their distribution is somewhat irregular, they more or less radiate in their general direction from the point at which the duct enters the intestine, which in the *rabbit* is nine inches or a foot from the pylorus. That part of it which occupies the duodenal mesentery must be considered the representative of the duodenal portion, and that spread out in the omentum underlaying and attached to the stomach, as the gastro-splenic. Altogether, this arborescent pancreas of the *Rodents* is very voluminous, particularly in the *rat*, from which the drawing was taken.

The pancreatic duct has in Mammalia generally the same branched character as in man, the greater and lesser branches corresponding to the lobes and lobules; usually there is but one orifice, rarely more, and most commonly it enters the intestine near the pylorus, although sometimes a great way removed from it. In most of the *Carnivora* it is, as a rule, united with the choledoc duct: in some cases it presents at the point of its immergence into the intestinal canal a sort of ampulla, in which the secretions probably mingle before their entry into the intestine. There are, however, considerable varieties of insertion — in the lion two pancreatic ducts join the choledoc separately, one near the other. But whether the ducts enter by a common orifice, or by two neighbouring ones, or whether there are one or two pancreatic ducts, has, probably, no physiological import whatever, as it cannot make any difference whether the secretions are brought into contact just before or just after entering the bowel; and this belief of the non-essential character of these varieties is strengthened, or rather proved, by their occurrence in closely allied species of the same genus, and even in different individuals of the same species. Cuvier says that he has observed, although very rarely, in the domestic cat, a lateral reservoir for the pancreatic secretion, analogous to the gall bladder. Its duct, about the size of the cystic, was an inch and a half long before it united with a trunk formed by the union of two pancreatic ducts, a principal and an accessory, and, together with this, formed a common duct analogous to the ductus communis choledochus. Tiedemann has detected a similar pancreatic reservoir in the common seal. The greatest distance from the pylorus at which the pancreatic duct enters the intestine occurs, I believe, in the *Rodents*. In the rabbit this distance amounts to a foot or upwards; and this arrangement, by giving a considerable length of small intestine whose contents are not acted on by the pancreatic secretion, has afforded special facilities for experiment.

* See the physiological portion of this article, page 104.

III. Physiology.

Anatomy always implies physiology, — structure, function; and the mind passes from the one to the other by a ready and almost irresistible transit. In fact, organisation is but the accumulation, in certain parts, of certain material agents, the sum of whose common action gives as its result the function of the organ, and both the nature of the elements so accumulated, and the method in which they are built up, are determined by, and have sole reference to, the work to be done. Physiology invariably stands to anatomy, even in its ultimate and minutest details, in the relation of final cause. Now, there are certain anatomical conditions that always indicate physiological importance; among these are *volume* and *constancy*, — constancy in existence, and constancy in structure. In all these respects we should be led to infer from the consideration of the anatomy of the pancreas that it possesses essential functions; for it is always of considerable size, has a very wide range of existence, throughout the whole of Vertebrata, from the lowest fish to the highest mammal, and is analogically represented in many Invertebrata; and, lastly, in structure it exhibits with very few exceptions, throughout this wide range, a remarkable sameness.

The opinions entertained by the old anatomists with regard to the office of the pancreas were many and various. The earliest anatomical writers do not seem to have been aware of its existence*; some thought that its object was to underlay the stomach as a cushion or pillow, and to serve for the distribution of vessels; others, that it admitted the chyle from the intestines; others, that it purified the dregs of the chyle; others, that it served for the spleen a purpose analogous to that of the gall bladder for the liver; others, that by it were thrown off the gross and used-up dregs of the blood; others, that the organ was formed for the reception of the excretion of the nerves; others, finally, taught that the pancreatic secretion was not only useful, but played a vital and essential part in the organism. The first opinion, which was of very ancient date, was held by Vesalius†; but it is at once refuted by a reference to those animals, birds and fish, for example, in which the pancreas is frequently remote from the stomach. The second view, that the pancreatic duct admitted the chyle from the intestines, is assigned to Baccius and Folius, who both maintained that it

* Hippocrates nowhere mentions it.

† De Humani Corporis Fabrica, i. 5. cap. 4. De Omento.

served for the transit of the chyle from the intestine to the liver and spleen. Very early investigation, however, showed the fallacy of this view, as it proved that the fluid of which the pancreatic duct was the channel always passed *to* the intestine and never *from* it. The fourth opinion is ascribed to Veslingius, who says, in speaking of the pancreas*, *Usus hujus canalis obscurus non est, nam cum acrem quendam felliqne non dissimilem succum exhibeat, palam est excrementum tale, per coctionem ulteriorem a chylo separatum, allici intra hunc atque in duodenum intestinum expurgari.* This view, which is simply refuted by saying that the secretion obtained from the pancreas does not in any way resemble bile, that it is not "felli non dissimilem," was supported by Asellius, Riolanus, and others. De Graaf accounts for it by supposing that the tube introduced into the duct for the purpose of obtaining the secretion became covered with the bile accumulated about the common orifice of the two ducts, which it might very well do, either on being inserted or withdrawn, and that this, becoming mixed with the pancreatic secretion which it had withdrawn, gave rise to the erroneous opinion that that secretion had a resemblance to bile. The fourth opinion, that the pancreatic duct was the excretory canal of the spleen, which was maintained by Bartholini, is refuted by the simplest anatomical considerations, and was further disproved by De Graaf, who, to show its fallacy, extirpated the spleen of a dog, and, two months after the extirpation, obtained the pancreatic secretion unaltered. The fifth view was based on similar supposed anatomical relations between the pancreatic duct and spleen. It is assigned to Lindanus, and was refuted by the same considerations as the last. The theory that the pancreas carried off the excretion of the nerves was based on the old view that the nerves distilled the animal humours and spirits. All these views are perhaps rather amusing than interesting, and are among the curiosities of science. They show us how much our medical forefathers were disposed to take for granted, and how disposed they were to run alone when the shell was still on their heads. The true doctrine that the pancreas furnished an important secretion of its own was first advocated by François de le Boë Sylvius †, who first insisted on its acidity, and who attached great importance to its pathological conditions. Indeed, he made its derangements the cause of nearly all the ills that flesh is heir to; in the same way that Spigelius did his lobe of the liver. It was in consequence of the interest which the lessons of Silvius excited that De Graaf, his pupil, undertook his admirable researches *De Succo Pancreatico*, and succeeded, in 1662, in first obtaining the pancreatic secretion from the living animal: the most important point was thus ascertained, and the materials supplied for further investigation.

* Syntagma Anatom. cap. 4.

† Thes. 37., De Usu Lienis et glandular.

With the view of obtaining the fluid, De Graaf first put a ligature round the duodenum, including part of the pancreas, but failed in obtaining the desired result, in consequence, as he imagined, of the ligature about the pancreas cutting off the supply of blood from which the secretion was obtained, and so putting a stop to it. He then put a ligature round the duct at the point of its immergence into the intestine, but again failed in getting any secretion, which he attributes to its escape by the small ducts wounded in exposing the larger one. His third attempt consisted in binding together two pieces of wood, compressing the intestine over the point of entrance of the duct so as to close it. This time he was successful: the duct was distended with a clear and limpid fluid, but he could not obtain it in sufficient quantity to subject it to any examination. With the view of obtaining some notable quantity, he instituted a fourth experiment by making a longitudinal incision into the duodenum, and inserting into the orifice of the duct the narrow mouth of a little flask; but again he failed, from the air included in the flask barring the entrance of the secretion. To obviate this, in his fifth experiment he perforated the upper part of the flask with a little hole, and this time he succeeded, in the space of five hours, in getting the flask more than half full. But the secretion obtained was bitter in taste and yellow in colour, and, attributing this to a certain admixture of bile from the uncleansed intestine, he improvised the following ingenious apparatus to obviate that source of fallacy. He took a long-necked flask, with a hole bored in the upper part of its belly, and around the neck of this flask he fastened a cord furnished with rings, by means of which it could be firmly fastened to the intestine; a quill of a wild duck, cut so as to form a little slender tube, was then fixed into the neck of the flask, and made to fit tightly by pasted paper being rolled round it. Into the smaller extremity of this quill tube was fixed a plug made of some soft wood fitting sufficiently tight not to be forced in by the pressure of the soft parts it would come in contact with, but sufficiently easy to be withdrawn by a string fastened to it, and which passed through the quill into the flask and out of the flask through the little hole. The object of the plug was to prevent the intestinal contents from blocking up the quill and so obstructing the flow of the pancreatic secretion. Then ("sublato ejulatu vicinis molesto, duarum laryngis cartilaginum particulas exscindendo," as he says of the poor dog with great simplicity and coolness) the abdominal cavity is laid open, an incision is made into the duodenum, the quill, closed with the little plug, inserted, the flask sewed to the intestine by means of the rings, the parietes sewed up so as to allow the protrusion of the flask, the plug withdrawn by the string, and the flask covered so as to prevent the entry of any foreign matter through the little hole. To obviate the escape of the secretion through a second pancreatic duct, which, he says, he found very common, he closed this second orifice by an ingenious method of compression. With this apparatus he succeeded in getting a free supply of pancreatic fluid, as clear as spring water, but slightly viscid, and varying in taste, from salt to acid, rough, acidulo-saline, or insipid. De Graaf's memoir is well worth reading, and is, considering the time in which it was written, and in spite of the necessary admixture of a good deal of mediæval physiology, a model of sagacious forethought and patient research. He insists strongly on the acidity of the fluid, not only in the dog, but in man, and affirms that he and many others found it to possess an acid taste in a man who had been suddenly killed, and whose body was still warm. But it is necessary to bear in mind his coarse and superficial means of examination, and the bias with which he undertook his researches from his strong attachment to both the physiological and pathological views of Sylvius.

Schuyl*, also a disciple of Sylvius, adopted a process analogous to that of De Graaf, and succeeded in obtaining a quantity of the secretion, amounting to two or three ounces, in three hours; he pretends that what he collected had an acid taste, and affirms, moreover, that it coagulated milk. The researches of Wepfer†, Pechlin‡, Brunner§, and Bohn|| did not confirm the assertions of De Graaf and Schuyl. These observers found the pancreatic secretion turbid, whitish, not acid, but having a taste slightly saline, like that of lymph. Succeeding experimenters agreed no better with regard to the qualities of this liquid. Viridet¶ said that he found it acid in most animals, and pretended that it sensibly reddened litmus. Hauermann**, on the contrary, denied that it had this effect. Fordyce†† found that of the dog to be colourless, watery, and salt in taste, and affirmed it to be composed of water, mucus, soda and phosphorus. Meyer‡‡ has examined the pancreatic juice in a cat, which he found in the vesicular reservoir which is sometimes met with in that animal. It appeared transparent, viscid, and had an alkaline taste; it coloured the mallow dye red, and red litmus paper blue. Meyer says further that he found in it albumen, chlorides of sodium and ammonia, and a peculiar matter giving a violet precipitate, with chloride of tin. Lastly, Magendie found§§ the pancreatic juice in a dog to be yellowish, inodorous, and with a saline taste. He adds that the liquid is alkaline, that it coagulates with heat, and that in birds it is altogether albuminous; at least, that, exposed to heat, it coagulates like albumen.

With such various opinions as to the qualities of the secretion, it is not surprising that the views of its function should have been discrepant, and accordingly we find that many hypotheses, often far-fetched and extravagant, were adopted to explain the part which the pancreatic fluid played in digestion. Some thought that it had for its destination the separation of the chyle from the excrements; others, that it served to temper the acridity of the bile; others, again, thought that it diluted the chyme, or that it dissolved that portion of the food which had not been digested in the stomach; that it contributed to its assimilation, &c. Haller, after exhausting himself with conjectures, can only say, "Plura possunt esse officia liquoris nondum satis noti;" and Magendie, fifty years later, admits that it is impossible to say what the *rôle* of the pancreatic fluid may be.

Such, then, were the opinions expressed, or rather the ignorance confessed on this subject, when in 1823 the Academy of Paris proposed the function of digestion as the subject of a prize dissertation, and two of the essays sent in, which were considered by the Academy worthy of honourable mention — the one by Professors Tiedemann and Gmelin, and the other by MM. Lenret and Lassaigne — threw so much additional light on the subject, and furnished results which so long constituted the staple of our certain knowledge of the function of the pancreas, and so much of which still remains unquestioned, that they deserve special consideration.

Lenret and Lassaigne, thinking that the failures of recent experimenters to get any of the secretion arose from the smallness of the duct in the animals employed, selected the horse, and succeeded in obtaining three ounces in half an hour of a limpid liquid, with a slightly salt taste, alkaline reaction, specific gravity of 1·0026, and containing ·9 per cent. of solid matter. Sulphuric, nitric, and hydrochloric acid slightly troubled it, and alcohol formed a more abundant cloud, precipitated after a time in white flocculi; an aqueous solution of chlorine determined a light flocculent precipitate; infusion of gall-nuts occasioned a yellowish deposit; lastly, nitrate of silver and protonitrate of mercury showed the existence of chlorides, and oxalate of ammonia that of lime. On treating the solid residuum with alcohol and evaporating, it yielded a transparent viscid matter, with a salt and sharp taste, the non-crystallizable portion of which consisted of an azotised substance precipitable by many metallic salts and solution of gall-nuts. That portion of the residuum of the pancreatic juice which had been exhausted by the alcohol was then heated with distilled water, when this latter showed on evaporation a certain viscosity, indicating the solution of an animal principle in it. The result of the entire qualitative analyses, the further details of which I need not give, was as follows: —

* Tractatus pro Veteri Medicinâ. Leyde. 1670.
† De Cicuta Aquatica, p. 200.
‡ De Purgantium Medic. Facult. Leyde. 1672.
§ Experimenta Nova circa Pancreas. Amst. 1683.
|| Circulus Anatomico-physiologicus. Leipsig, 1710.
¶ De Primâ Coctione, p. 266.
** Physiologie, th. iii. p. 807.
†† Versuche über das Verdauungsgeschäft, Leipsig, 1793.
‡‡ Journ. compl. et Dict. du Sc. Méd. t. iii. p. 283.
§§ Précis Elémentaire de Physiologie, t. ii. p. 267.

Water - - - -	99·1
Animal matter soluble in alcohol -	00·9
Animal matter soluble in water -	
Traces of albumen - -	
Mucus - - - -	
Free soda - - -	
Chloride of sodium - -	
Chloride of potassium - -	
Phosphate of lime - -	
Oxide of iron - -	a trace
	100·0

"Not content," say these observers, "with this first experiment, we undertook a second with the same success*, and the results furnished by analyses were absolutely the same: from which we infer that the pancreatic juice possesses a perfect analogy with the saliva both of man and the horse, these two liquids containing absolutely the same fixed principles, nitrogenous and saline, and almost exactly the same quantity of water.† The attempts of these authors to obtain the pancreatic secretion of a dog, after the manner of De Graaf, were all unsuccessful; ten times they tried, and as often failed; a few drops were all they could procure. Their data, therefore, are all taken from the secretion as they found it in the horse.

Tiedemann and Gmelin ‡ obtained the pancreatic fluid from the dog, the sheep, and the horse—that is, from one carnivorous and two herbivorous animals; and their results present the most striking discrepancies with those of the contemporaneous experiments of Lenret and Lassaigne. In the dog this fluid, which was obtained abundantly, was limpid, with a faint blueish, opalescent cast, and a mucilaginous feeling like the white of egg diluted with water, a slight but sensibly saline taste, the first portion faintly *acid*, the portion last secreted slightly alkaline, and so abundantly albuminous as to be rendered semi-solid by heat nitric acid, &c. A hundred parts of the secretion contained —

Solids - -	8·72
Water - -	91·28
	100·00

100 parts of solid matter contained

Organic substances, osmazome with a peculiar animal matter coloured red by chlorine (with alkaline acetates and chlorides) - -	44·32
Caseous substance, possibly with another animal substance, soluble in water, but not in alcohol (with salts of soda) - -	18·44
Albumen, with a small quantity of salts - - - -	42·83
	105·59
Exceeding -	5·59

* They do not say the quantity they obtained this time.

† Loc. cit. p. 106.

‡ Recherches Expérimentales Physiologiques et Chimiques sur la Digestion. Jourdan's translation, p. 24. et seq.

The secretion of the sheep was acid, and, like the other, ropy between the fingers like white of egg, and limpid; it was perfectly solidified by heat, and contained —

Solids (desiccated)	5·19
Water - -	94·81
	100·00

Of these solids nearly 60 per cent. were albumen. The secretion in the horse resembled in all its reactions that of the sheep, except that the albumen was not so abundant.

The summary conclusions at which these authors arrive, are that the pancreatic fluid contains —

1. In solids, in the dog 8·72, in the sheep 5 per cent.
2. The solids consist of —
   a. A large amount of albumen, about half of the dry residuum.
   b. Osmazome.
   c. A substance reddened by chlorine, found only in the dog.
   d. A caseous substance, probably allied to salivary matter.
   e. A small amount of free acid, probably acetic, present in all these specimens. It is worthy of remark, that that portion of the pancreatic fluid which was secreted last was slightly alkaline: this change probably depended on the enfeeblement of the nervous influence resulting from the operation.
   f. The ash consisted of alkaline carbonate, chloride, phosphate, and sulphate, and carbonate and phosphate of lime.
   g. The alkaline sulpho-cyanide is not met with in the pancreatic secretion.
   h. The alkali consists of a *large quantity of potash*, and a very *small portion of soda* salts.

If we compare the composition of the pancreatic secretion in the dog and the sheep with that of the saliva, we find the following differences:—

1. The solid residue of the saliva does not equal half that of the pancreas.
2. The saliva contains mucus and a peculiar animal (*salivary*) matter. If it contains albuminous or caseous matter, these subtances are, in every case, in very small quantity. On the contrary, the pancreatic fluid contains an abundance of albumen and caseous matter, but not a trace of mucus, and true salivary matter, if it exists, is in very small quantity.
3. The saliva is neutral, or contains a little alkaline carbonate. The pancreatic secretion contains a little free acid.
4. The saliva contains sulpho-cyanide of potassium; in the pancreatic fluid there is none.
5. The other salts are nearly the same.
6. It results, therefore, that those physiologists who think the pancreatic secretion identical with saliva are in error.

There is, then, an entire discrepancy between these two authorities with regard to the pancreatic secretion—its physical qualities, reaction, amount of solids, chemical constitution, the conclusions they infer, &c.

Very lately this subject has been taken up by several able physiologists, and Bernard*, Frerichs †, and Bidder and Schmidt ‡, have given to the world the results of careful and elaborate researches both into the physical and chemical characters of the fluid and its physiological action. I shall describe first the observations of these inquirers on the qualities of the secretion, and, afterwards and separately, their views of its physiological office. It is very remarkable, that the differences in the accounts given by these recent investigators are very closely analogous to those existing between the results of the researches above described. They all agree, however, as to the invariable alkalinity of the secretion, the absence of sulpho-cyanides, the existence of a specific nitrogenous principle, and, in general, to its possession of strong differential characters when compared with saliva.

According to Bernard, the pancreatic secretion obtained artificially during the life of the animal is of two very distinct kinds, which he characterizes as *normal* and *morbid;* the former obtained when the experiment is made under favourable circumstances, before inflammation has attacked the pancreas, or which is collected from a dog possessing a permanent pancreatic fistula; the latter always secreted in great abundance when the symptoms of inflammatory reaction appear in the pancreas and in the wound in the abdomen.

The *normal* secretion, which, adopting Bernard's view, is of course *the* secretion, he describes as a colourless, limpid, viscid, ropy fluid, without any characteristic odour, and having a saline taste very like that of the serum of the blood. It is constantly alkaline. Exposed to heat, it is converted into a solid white mass; the coagulation is as entire and complete as that of white of egg, the whole becomes solid, not a drop of free liquid remaining. The other reagents of albumen equally precipitate it. The alkalies produce no precipitate, and redissolve the organic matter when it has been previously coagulated by heat, alcohol, or the mineral acids. But, although exhibiting the same reactions, Bernard believes that this nitrogenous principle is essentially distinct from albumen, not only in a physiological point of view, but in its inherent nature; and, as a proof of this, he cites the fact, that when it has been coagulated by alcohol and dried, it is easily and entirely redissolved in water, whilst albumen, similarly treated, is not dissolved to any appreciable extent. § These characteristics of the fluid, which are given from the dog, Bernard says obtain equally in rabbits, horses, and birds. The *morbid* pancreatic fluid, which is alone thrown out when the experiment is tardily or roughly performed, and which always succeeds to the other when the experiment is happy, is watery, without any viscosity, has a saline and nauseous taste, is of very low specific gravity, and gives hardly any precipitate on the application of heat, nitric acid, &c. It is poured out very abundantly: Bernard collected from a dog more than half an ounce in an hour, whereas of the normal he found 31 grains a maximum. The normal is not transformed into the morbid secretion suddenly, but gradually, losing, as it becomes more and more watery, its physiological properties, of which at last it is quite destitute. This observation of Bernard's is very important, as showing the facility and extent to which the fluid may be changed, and doubtless it goes some way to explain the discrepancies of the accounts which different observers have rendered, but it is not entirely sufficient for this, as, in some hands, a watery fluid with but little albuminous matter and of very low specific gravity seems to have been obtained at once, even under circumstances the most favourable.

Frerichs, who has made a most complete analysis of this fluid *, and with whose account Lehmann † agrees, describes it as colourless, clear, very slightly tenacious, without taste or smell, of alkaline reaction and a specific gravity as low as 1·008 to 1·009; heat, alcohol, and acid, produce but a slight turbidity; of solid constituents he found it contain but 1·36 per cent. in the ass, and 1·62 in the dog.

Schmidt's account is something intermediate between the other two; he describes the fluid as ropy and viscid, and as being coagulated by heat into a milky mass, from which white flocculi subside, leaving above a clear, strongly alkaline fluid. He agrees with Bernard in the solubility by water of the precipitated and dried albuminous matter; he states the specific gravity of the fluid at 1·031, and the quantity of solid constituents at 9·924 per cent.; in one case the amount of solids reached 11·56 per cent.

The following are the quantitative analyses of Frerichs and Schmidt:—

Pancreatic juice of ass (Frerichs).

Water - - - -	986·40
Solid residue - -	13·60
Fat - - - - -	0·26
Alcohol extract - -	0·15
Water extract - -	3·09
Soluble salts - -	8·90
Insoluble salts - -	1·20

Pancreatic juice of dog (Schmidt).

Water - - - -	900·76
Solid residue - -	99·24
Organic matter - -	90·38
Inorganic - - - -	8·86

* Arch. Gén. de Méd., 4th Ser. tom. 19. p. 68—86.

† Wagner's Handwörterbuch der Physiol.

‡ Die Verdauunggeschäft und der Stoffwechsel, Leipsig, 1852.

§ Bernard believes this to be the active matter of the secretion, as it imparts to the water the peculiar viscosity and physiological properties of the pancreatic fluid.

* Op. cit. p. 842—849.

† Physiol. Chem. (translated by Day), p. 112. et seq.

The exact nature of Frerichs' *water extract* — Schmidt's *organic matter* — is not determined; it is *a substance resembling albumen or casein*, but not identical with albuminate of soda, with casein, or with ptyalin. It coagulates only imperfectly when heated (probably from its containing an alkali), is precipitated by acetic acid, but slowly redissolved in an excess, especially if heated; it is precipitated by nitric acid and by alcohol; on the addition of chlorine-water it separates in grayish flakes. It is to this substance that the pancreatic fluid owes its principal chemical and physiological properties.

Bernard found a considerable quantity, and Frerichs a smaller amount (·026 per cent) of a *butter-like fat*.

The pancreatic secretion is peculiarly prone to putrefactive change. Bernard found that when exposed to a low temperature, it might be kept for many days, and that by the reduction of the temperature the viscidity was increased, approaching a jelly-like firmness. If, on the other hand, it was kept at a temperature of 40° to 45° centigrade (about 105° Fahr.), it became rapidly modified, and in the lapse of a few hours quite altered, giving out a nauseous odour, presenting a cloudy deposit, and losing its property of coagulation by heat. In the heat of summer and in stormy weather, this change takes place almost instantaneously, so that great care is necessary in maintaining at a low temperature both the pancreatic fluid and the animal furnishing it, lest the alteration should take place whilst it is still in the vessel in which it is being collected. Frerichs found that after exposure to the air for a few hours it developed a distinct odour of putrefaction. Bernard observed that the deposit that was produced at the moment of the alteration of the fluid, had sometimes a peculiar soft, silky appearance, and he always found in that case, on examining it by the microscope, a large quantity of acicular crystals, having the characters of crystals of margarine or margaric acid.

The secretion is not constant, but intermittent, and is entirely regulated by the process and stages of digestion; all observers agree in this. Bernard killed three dogs in three different conditions with regard to the function of digestion — one just after a meal, as digestion was just commencing; another four hours after a meal, when digestion was at its height; and a third after a twenty-four hours' fast. In the first, the tissue of the pancreas was slightly turgid with blood, and the secretion the most abundant, and this he has always found to be the case; he collected upwards of two grammes an hour; in the second, the pancreas was highly turgid — "*gonflé de sang, et comme erectile*," and the amount secreted less than a gramme an hour; in the third it was white, exsanguine, the duct empty and collapsed, and the amount secreted in many hours hardly enough to moisten the inside of the little reservoir adapted for its reception.

The information respecting the absolute quantitative relations of the secretion is very defective. We have seen that Lenret and Lassaigne obtained three ounces from the horse in half an hour, and Bernard from the dog thirty-one grains an hour; Frerichs collected three hundred and eighty grains from an ass in three quarters of an hour, and forty-five from a hound in twenty-five minutes; but these statements, as well as those of Colin *, become valueless from the fact that the animals experimented on were not weighed. The most reliable estimate is that of Bidder and Schmidt; they say a dog yields a grain and a half per hour for every two lbs. of weight; therefore an adult man weighing about 140 lbs., would secrete in twenty-four hours nearly five ounces of pancreatic juice, containing 225 grains of solid residue. But it is doubtful whether any safe data as to quantity are furnished, or can be furnished, by any experiments made by measuring the amount procured artificially from the living animal; the abnormal condition of the gland produced by the experiment must be such, and the consequent disturbance of the secretion so great, as to throw doubt on the most careful and exact estimates. The case in which the quantity seems most likely to be normal is that in which the secretion is obtained, as in some of Bernard's experiments, from a permanent fistulous opening. All observers confirm Bernard's statement as to the exsanguine and passive condition of the gland in animals fasting.

The natural stimulus of the secretion is, no doubt, the digestive process going on in neighbouring organs, producing, through the medium of the sympathetic nervous connections, a vascular engorgement of the pancreas and an exalted nutrition of its secreting agents. Possibly the pressure from a distended stomach may have something to do with it; and there is reason to think that the presence of food in the duodenum is both a stimulus to the secretion and to its discharge; for on the application of chemical and mechanical stimuli to the inner surface of the duodenum near the orifice of the duct, the amount discharged is sensibly increased. Possibly food of one nature in the duodenum may be a more exciting stimulus to the secretion than another. Whether this is so, whether the amount secreted would be excited more by an animal than a vegetable food, whether it bears the same relation to the volume of the gland in Carnivora and Herbivora, or whether the volume of the gland is always a direct measure of the amount secreted, are questions upon which, as yet, our information is very defective. They are, however, not unimportant questions; for there is every reason to believe that the quantity secreted is always in proportion to the exigencies of the digestive process, and their solution might therefore throw some light upon the function of the secretion. There can be no doubt that muscular movement and pressure facilitate the *discharge* of the fluid, as most observers, from De Graaf

* Comptes Rendus, vol. xxxi. p. 374, and vol. xxxii. p. 85.

downwards, have remarked that the act of inspiration, and violent respiratory or struggling efforts, always increase the rapidity of its flow.

The following is a tabular view of the statements of different observers of the principal characters of the pancreatic secretion :

	Tiedemann and Gmelin.	Leuret and Lassaigne.	Bernard.	Frerichs.	Bidder and Schmidt.
General Physical Qualities.	Limpid with a blue-white cast, like white of egg diluted with water, slight, but sensibly saline taste.	Limpid with a slightly salt taste.	Colourless, limpid, viscous and stringy; odourless; taste saline.	Colourless, clear, *slightly* tenacious, without taste, or smell.	Clear, colourless, viscid and ropy.
Reaction.	Dog { at first slightly acid, after slightly alkaline. Sheep, slightly acid Horse, ditto.	Alkaline.	Always alkaline.	Alkaline.	Strongly alkaline.
Specific Gravity.		1·0026		1·008 to 1·009	1·031
Amount secreted.	At the rate of one ounce per hour in the dog.	Three ounces in half an hour—*horse*.	*Normal* 31 grains an hour. *Morbid*. 279 ditto.	380 grains in ¾ of an hour—*ass*. 45 ditto in 25 min. —*dog*.	1½ grain every hour for every 2 lbs. weight.—*dog*.
Quality of Solids.	Dog, 8·72 per cent. Sheep, 5·19 ,, ,,	·9 per cent.		Ass . . 1·36 Dog . 1·62	9·924 per cent.
Amount of Albumen, &c.	Rendered semi-solid by some of the reagents of albumen —*dog*. Perfectly solid by heat —*sheep*. Abundant consistent flocculi on heat —*horse*.	*Slightly troubled* by the reagents of albumen. Azotised principles soluble in alcohol and water. *Absolutely the same as saliva*.	Entirely solid by heat, as white of egg: also the strong mineral acids and alcohol. The dried precipitate may be re-dissolved in water. No sulphocyanides.	*Inconsiderable* coagulation on heating. *Slightly* turbid on adding alcohol and nitric acid. Butter-like fat 0·026 No sulphocyanides.	Alcohol coagulates it into a miky mass, which deposits thick white flakes, leaving above a strongly alkaline solution. The dried flakes dissolve in water.

Function of the pancreatic fluid.—The first indication of the importance of the pancreatic juice to the process of digestion has been assigned to Valentin. He showed that it converted into sugar that portion of the amylaceous matter that had not been acted on by the saliva and had passed unchanged into the duodenum ; and he ascertained that both the expressed secretion and an infusion of the gland-substance exercised this transforming property in a high degree. Bouchardat and Sandras found that the pancreatic secretion of fowls and geese possessed this property, and immediately transformed starch into dextrine and grape sugar. On raising the fluid to 100° (centigrade) it became inert ; but the flocculi precipitated, either by heat or alcohol, on being redissolved exerted an influence exactly the same as the original secretion, and with the same power. In this albuminous substance they recognise the material of which, under the name of *diastase*, they had indicated the existence in the alimentary canal of granivorous birds. They profess themselves unable to define the action of this substance compared with that of diastase. Like diastase it is nitrogenous; and they regard it as the principal agent in the digestion of feculent aliments. They found, moreover, that a fluid of similar properties might be obtained by macerating for a short time portions of the pancreas, finely minced, in an equal weight of water. The fluid thus prepared converted a thick starch jelly into a thin fluid, without any viscosity, in the lapse of a few minutes. By many alternate precipitations with alcohol and solutions in water, as in the operation for the purification of diastase, a flocculent precipitate was obtained, which, rapidly dried, possessed a very energetic solvent power. The existence of a principle acting like diastase on fecula was equally demonstrated in the rabbit, the dog, and man.*

Within the last few years an additional and most important office has been claimed for the pancreas by M. Bernard†—that, namely, of emulsifying or saponifying the neutral fatty matters contained in the food, by decomposing them into glycerine and their respective fatty acids, and so rendering them absorbable. M. Bernard bases his views on two methods of proof — on experiments on the living animal, and on the secretion after its removal ; and his whole paper is characterised by an admirable completeness and most orderly logic. The first series of experiments consists in the admixture of various fatty matters — olive oil, butter, tallow, lard — with fresh pancreatic juice, alkaline, viscid, and possessing all the characters of the *normal* secretion ; a temperature about that of the body is applied, if necessary, and the mixture agitated. In every case a smooth, creamy emulsion is at once produced. In keeping the products of these experiments at a temperature above 100° Fahr. for fifteen or eighteen hours, he says the emulsion was perfectly maintained ; the appearance of the white creamy liquid was quite unchanged, nor was there, although kept in perfect re-

* Compt. Rend. t. 20. p. 1085.

† Archives Gén. de Médecine, iv. serie, t. 19.

pose, any separation between the pancreatic fluid and the fatty matters. After the lapse of some hours it became evident that the fat had not only been minutely subdivided and emulsified, but that it had, furthermore, been chemically modified. In fact the neutral fatty matter and the alkaline pancreatic juice, constituting at the moment of mixture a white liquid with an alkaline reaction, had, five or six hours afterwards, acquired a reaction distinctly acid. In examining what had taken place, it was easy to show, by the ordinary means, that the fatty matter had been decomposed into glycerine and a fatty acid. In the test-tube in which the butter had been subjected to the action of the pancreatic fluid, the butyric acid was easily recognised, even at a distance, by its characteristic odour. Bernard then goes on to prove, by the method of elimination, the unicity and propriety of this property of the pancreatic secretion, by showing that no other fluid in the body — bile, saliva, gastric juice, serum, the cephalorachidian fluid — is capable of exciting it: all these fluids mixed with the various fatty matters failed in producing an analogous effect in any degree.

This instantaneous emulsion, however, of neutral fatty matters, and their separation into glycerine and a fatty acid, is only effected by *normal* pancreatic juice; that is to say, a pancreatic juice, alkaline, viscid, and coagulating in a mass by heat or the strong acids. If, on the other hand, the oil is mixed with a *morbid* or *altered* specimen of the secretion — that is, watery, without viscosity, and not coagulating by heat,—its action on the fatty matters is nil, and a speedy separation takes place between the inert pancreatic fluid and the unmodified fatty matter.

Taking as a postulate the admitted fact, that it is the white, opaque, milky chyle alone that contains fatty matter, Bernard then proceeds to show by experiments on the living animal, that fatty matter thus modified alone finds its way into the lacteals, is alone absorbable, and that it is the pancreatic juice only that is capable of effecting this change. In all dogs killed in mid-digestion of fatty aliments, the fat was merely *fluidified* by the heat of the stomach, retained all its characters, and, on the application of cold, congealed on the surface of the gastric juice like the fat on broth. In the intestine, on the contrary, below the openings of the pancreatic duct, the fat could not be distinguished by these characters, but formed a pultaceous, creamy, emulsive material; and the lacteals were gorged with a white, homogeneous, milky chyle. But when the pancreatic ducts were tied, the fat remained unaltered in the intestine, and the lacteals contained nothing but a limpid chyle free from all fatty material, which had ceased to be absorbed in consequence of the abstraction of the pancreatic secretion.

Furthermore, in the rabbit (in which, by an arrangement altogether exceptional, the pancreatic duct opens into the intestine at a distance of 10 or 12 inches from the pylorus), another proof of the same fact may be obtained without any ligature or mutilation. If a rabbit be crammed with lard, and the intestines examined in mid-digestion, the fat contained in the small intestine above the opening of the duct will be found unchanged, while that immediately below and downward has undergone the emulsifying process. The lacteals, also, above that point are filled with a limpid chyle, while those arising immediately below are conspicuous for their milky, opaque contents. It is impossible, as Bernard says, to find, in the whole range of experimental physiology, a more elegant and simple method of proof.

The tardiness of physiologists in the discovery of this function may be explained, Bernard thinks, by their minds being preoccupied with the false notion that the pancreatic secretion was analogous to the saliva; and the assignation of this function to the bile by Sir Benjamin Brodie, he accounts for thus. Brodie performed his experiments on cats, and found that, after ligature of the choledoch duct, the lacteals contained no fat, and that the chyle was limpid and transparent. Shortly after, Magendie, with the view of verifying these experiments, repeated them on dogs, but found that the absorption of the fat and the whiteness of the chyle were in no way interfered with by the ligature of the gall-duct. Now in cats the pancreatic duct joins the choledoch before it enters the intestine; so that it is conceivable that Sir Benj. Brodie, having only in view the action of the bile, and attaching no importance to the pancreatic canal, had tied the one with the other: and thus the absence of fatty matter in the chyle may be explained. But in dogs the choledoch is completely separate from the two pancreatic ducts, so that after its ligature the flow of the pancreatic juice remains perfectly free, the fat continues to be emulsified, and the chyle to possess its characteristic whiteness. These experiments, therefore, are entirely in accord, and the difference of their results is strictly assignable to the different disposition of the ducts in the animals on which they were respectively performed.

Some little time ago, while engaged with Dr. Todd in some investigations upon this subject, I tied the gall-duct in some score of dogs, and invariably found that its ligature in no way interfered with the absorption of the fat and the perfect elaboration of the chyle. As long as the supply of the pancreatic secretion was not interfered with, the emulsifying of the fat was complete, and its absorption entire. I also repeated Bernard's experiments on rabbits, and obtained results in perfect accord with his views. I injected melted lard into the stomach, then gave them a meal of green food, and killed them in three or four hours. The point of immergence of the pancreatic duct was most distinctly that of the commencement of the opacity of the chyle: the lacteals above were filled with a fluid clear and limpid.

But these views, so neat and complete in themselves, and so nicely put forth by Bernard, have of late been vigorously assailed by the German school, and their fidelity and conclusiveness altogether impugned. Frerichs, and Bidder and Schmidt, have, by a repetition of Bernard's experiments, as well as by many ingenious and well-devised ones of their own, failed to verify any of his results, but have been led by them to conclusions with which they are altogether discrepant. These experimenters state that they carefully followed all Bernard's directions — they tied the pancreatic duct, and, having previously kept the animals on short food from twelve to twenty-four hours so that there might be no remains of the secretion in the intestine, fed them with fatty aliment, and killed them in from four to eight hours. They always found the lacteals "most beautifully injected, and the receptaculum chyli distended with milky chyle."

Frerichs found on tying the small intestine some distance below the opening of the pancreatic and bile ducts in cats and puppies, and injecting into the bowel below the ligature olive oil and milk, that after two or three hours the lacteals were filled with white chyle. He, however, believes that he has found the extreme comminution of fat, and hence in some measure its resorption, promoted by the bile and pancreatic juice; for when in cats that had long fasted, he cut through the small intestine near the middle, injected olive oil into both halves, and tied the two cut extremities, he found the lacteals springing from the upper part of the intestine always far more injected than those proceeding from the lower, which he attributes to the bile and pancreatic juice having access to the fat in the upper portion.

With regard to the permanence of the emulsion produced by the mixture of pancreatic juice and fat out of the body, Frerichs and Bernard are quite at issue; for while Bernard states, that on being examined fifteen or eighteen hours afterwards, it was found to be perfectly maintained, Frerichs affirms that the particles of oil soon separate again on the surface.

There certainly are some circumstances which detract from the conclusiveness of Bernard's experiments: one is, that the chyle contains far less fatty acids than the ordinary neutral fats; another, that other animal fluids, as soon as they begin to putrefy, cause a similar decomposition of the neutral fats; another, that Bernard's experiments merely had reference to the production of this change *out of the body*. This last deficiency has been filled up by Lenz.* He fed healthy cats with fresh butter, or, if necessary, injected it into their stomachs, and killed them in from six to fourteen hours afterwards. Although all the lacteals and the thoracic duct were distended with milky chyle, no trace of butyric acid could be detected in the stomach and intestinal canal, or in the thoracic duct, the portal vein, or gall-bladder. By further experimental investigation, he found that the metamorphic action was hindered by the acid gastric juice in proportion to the amount of free acid present, that a similar action might be artificially induced by other acids, as diluted lactic, tartaric, and acetic acid, and that it might be overcome by neutralising the free acid by bile, or by an alkali. Hence he concluded, that it is only in exceptional cases that the pancreatic fluid decomposes the neutral fats into acids and bases in the living body.

The argument derived from the experiment on rabbits has been thus explained away by Bidder and Schmidt. They say that if the rabbit is killed two hours after the fat has been given it the lacteals given off *between the pylorus and the mouth of the pancreatic duct*, are fully distended with white chyle very rich in fat; if not till four hours after the injection, the lacteals situated about three or four inches above the mouth of the duct are still filled; if at six hours, those only below the duct contain white chyle; and if not till eight or ten hours after, the first lacteals well injected with milky chyle are found to be situated ten or twelve inches below the duct. Hence it must have been by always killing the animals six or eight hours after feeding them with fat, that Bernard was able apparently to maintain his view. The facts of the case, say they, were simply these. The chyle had already passed onwards from the lymphatics proceeding from the first portion of the duodenum, and there was no more fat to be absorbed in that portion of the intestine when Bernard began the investigation. I cannot admit the correctness of this explanation given by Schmidt and Bidder, because some of the rabbits on which I repeated Bernard's experiments and verified his results were killed within four, or even three hours after the injection of the lard.

It was formally maintained by MM. Bernard and Barreswill, that the pancreatic juice when acidified had an equally solvent power on the precipitated protein compounds with the gastric juice, and that its acidity or alkalinity alone determined whether it should act on albuminous or amylaceous matters. This opinion has also been refuted by Frerichs.

Lastly, this physiologist ascribes to the pancreatic fluid a peculiar power of hastening the conversion of the bile into insoluble products, and so favouring its more perfect elimination. This view has been completely overthrown by the experiments of Bidder and Schmidt, who have shown, first, that the greater part of the bile is not thrown off with the fæces, as Frerichs believes; and, secondly, that the lime, to which Frerichs especially ascribes this power, only exists in very subordinate quantity in the pancreatic fluid.*

In taking a review of all that has been done with regard to the functions of the pancreatic secretion, we must admit that the only one that has been established beyond dispute is its sugar-making action on amylaceous matters.

* De Adipis Concoctione et Absorptione. Inaug. Diss. Dorp. Liv. 1850.

* British and Foreign Med. Chir. Review. On the "Chemistry of Digestion," by Dr. Day.

The whole subject is singularly full of contradictions and discrepancies, and it must be confessed is also singularly full of sources of fallacy. If Bernard's description of two kinds of pancreatic fluid, normal and morbid, be correct, it may go a great way to explain why those who, like Frerichs, have experimented with a watery fluid, poor in albumen, have failed to verify his results, and therefore it will vitiate their objections. It is almost impossible to help seeing something like a national bias in the adoption of one or the other set of opinions; for while Lehmann follows Frerichs and Schmidt and Bidder, the French physiologists as implicitly adopt the views of Bernard, and confirm his results. Even the action on starch, though *a* function of the secretion, can hardly be said to be *the* function; for the relative size of the gland is greater in carnivorous than in herbivorous animals (the weight being $\frac{1}{300}$th of that of the whole body in dogs and cats, and only $\frac{1}{600}$th in that of rabbits*), and further, as Bidder and Schmidt have shown, the greater part of the amylaceous food of the sheep is converted into sugar before it enters the duodenum. With such patent facts as these, and with objections to Bernard's views so many and so grave, I feel disposed to adopt the words of the learned translator of Lehmann, and say, that "we may fairly conclude that the *principal* uses of this secretion are still unknown."

V. Morbid Anatomy.

The interest that attaches to the deranged anatomy of the pancreas is the interest of obscurity — the interest of diagnosis; I may add, too, the interest of situation; in fact, it is from the situation of the organ that the importance and obscurity of its pathological relations at once result. Close to the stomach, duodenum, liver, spleen, kidney, aorta, cava, mesenteric glands, and cœliac axis, it finds itself in immediate relation with the great vascular, nervous, digestive and absorbent centres of the abdomen, and may either affect them secondarily, be affected by them, or furnish a source of fallacy and doubt as to whether it be it, or they, or both that are implicated: and while it is thus placed at the most important point in the whole range of *medical* anatomy, its situation almost completely precludes it from the advantages of physical diagnosis.

The pancreas enjoys an immunity from disease greater than most organs, but I believe this immunity is in part real and in part only apparent; for it cannot be doubted that one reason why the records of its morbid anatomy are so scanty, is that in so large a number of post-mortems, no examination of the organ is made at all. It is the last to be got at, and the cause of death having been ascertained, its examination is looked upon as supererogatory; besides, it is often obscured and mutilated in the removal of other organs, and its careful dissection from its situation, which is necessary to examine it satisfactorily, is troublesome and not very easy.

Its simplest morbid conditions, and most common, are those of —

a. Quantitatively perverted nutrition — hypertrophy and *atrophy*, *induration* and *softening;* and the commonest of all is,

Hypertrophy. — It is difficult to say precisely at what point hypertrophy of the pancreas commences, because the limits within which the size of the gland may normally vary are so extensive that a considerable excess of volume is evidently quite consistent with anatomical and functional health. Generally, the hypertrophy is not pure, but is associated with some induration; and in the majority of cases both the induration and hypertrophy appear to result from chronic inflammation, giving rise to some increase in the proper gland structure, but more to an effusion of lymph between the lobes and lobules by the partial organisation of which a great increase in the amount of the interlobular tissue is produced. This gives rise to an appearance of intersection by opaque membranous septa, giving the gland a scirrhoid character; and hence, by some this morbid alteration has been considered as the first step towards scirrhous degeneration, and by others as actual scirrhus. Whenever the colour of an enlarged pancreas is deeper and redder than natural it may be inferred that the hypertrophy is due to this chronic inflammatory action. Sometimes the enlargement is slight, sometimes it is very great. Dr. Fearnside* mentions a case in which the gland was four times its natural size, and could be felt as a large tumour during life, although the emaciation was not extreme. The results of the hypertrophy are very various; sometimes it gives rise to jaundice by pressure upon the gall-ducts; to dilatation of the stomach, dyspepsia, &c., by pressure on the duodenum and pylorus; to occlusion, even, of its own ducts†, and to many disturbances, functional and organic, of neighbouring parts, produced by its altered volume and relations.

Atrophy of the pancreas, mere diminution of volume unaccompanied by any other change, is sometimes idiopathic, but much more frequently caused by neighbouring disease, as for example, the pressure of some tumour. Morgagni found the pancreas atrophied from the pressure of a tumour in the liver. Dr. Hall found the same condition caused by a

* It is a singular thing that the very reverse of this fact, the assertion, namely, that the pancreas was larger in herbivora than carnivora, was advanced by Valentin in support of his views of the metamorphic action of the pancreatic fluid on starch. I had myself made some extensive tables of the absolute and relative size of the pancreas in carnivorous and herbivorous animals, and carnivorous and granivorous birds, those of a mixed diet, and in reptiles, also in young and old of the same species, but they are unfortunately lost; all I can say from recollection is, that in conformity with the statement in the text, I found the gland largest in carnivora, smallest in vegetable feeders, and intermediate in those of a mixed diet; its relative size was also inversely as the age, though apparently in no regular ratio.

* Medical Gazette, vol. xlvi.

† Copland's Med. Dict., art. Pancreas.

scirrhous tumour in the mesentery. M. Guerin observed this lesion produced by a similar cause. M. Berjaud by aneurism of the aorta; and M. Mondiere by scirrhous pylorus. In some cases it seems to be produced by arrest of its function, as when scirrhous disease of the pylorus has put a stop to the passage of food into the duodenum. Dr. Wolf mentions a case in which the atrophy seems to have been produced by the ossification of the pancreatic arteries and obstruction of the duct. I do not know if there are any symptoms by which idiopathic atrophy declares itself during life, and in those cases in which it is secondary, the symptoms are those of the primary disease and not those of the pancreatic affection. The degree of wasting is sometimes very great; Cruveilhier met with a case in which it did not exceed an ounce in weight.

Induration. — Sometimes the pancreas is found of a firmer consistence than natural, without any perceptible alteration in structure. It has been alleged that in these cases it is the secreting structure that is affected, the areolar tissue not being implicated in the induration, which imparts to the gland a more nodular or granular appearance and feeling. But whether this is so, I cannot say, as I have never submitted an indurated pancreas to microscopical examination. It is said to be not uncommon for induration of this kind to disappear, as happened in a case recorded by Mr. Lawrence, soon after exposure to the air.

Softening has been found to occur chiefly in persons suffering from scrofulous affections. Portal relates that he found the gland remarkably softened without any other change, in two children who died of measels. In confluent small-pox and malignant scarlet fever softening of the pancreas has occurred. Dr. Copland states that he has found it softened in cases of malignant remittent fever and scurvy, but only in conjunction with softening of other organs, as the spleen, &c.

b. Inflammation. — The number of cases in which post-mortem appearances of *acute* inflammation of the pancreas have been recorded is certainly very small. When it does occur the appearances are said to be great injection of the whole gland, imparting to it a brown-red colour and an unnatural softness and friability. In a case recorded by Mr. Lawrence, this brown-red colour presented a strong contrast with the pale anæmiated condition of the other parts. When the inflammation does not end in resolution, it may give rise to the *effusion of plastic lymph* on the surface, producing a general or partial false capsule, or to the *formation of pus* in its substance—pancreatic abscess. It is also *said* to end sometimes in *gangrene.*

In consequence of the effusion and subsequent organisation of coagulable lymph upon the surface of the pancreas it has occasionally been covered by a false membrane of great consistence. By the extension of the adhesive inflammation to some of the neighbouring organs, as the stomach, duodenum, liver, spleen, mesentery, mesocolon, &c., bands are occasionally formed, connecting the pancreas to one or more of these organs, which sometimes acquire so great a degree of hardness, as to be with difficulty divided with the scalpel.

In suppurative inflammation, whatever may have been its point of commencement, the pus is ultimately infiltrated into the interlobular tissue, and when the process of suppuration is completed, is generally collected into one cavity. In most cases, the inflammation being but partial, this cavity is of moderate size; but sometimes the suppuration proceeds to such an extent that the texture of the gland is almost entirely destroyed. In some instances, this destruction being complete, the purulent matter is contained in a membranous envelope, formed by the cellular tissue which covers the organ. Portal has seen more than two pounds of pus contained in a sac of this description. The character of the purulent matter in such cases seems to be various. According to Gendrin it is commonly inodorous and creamy; Portal, on the other hand, states that in complete suppuration of the pancreas, the pus is sometimes of an intolerable smell; not unfrequently it is combined with a clear yellowish fluid, and with a whitish curdy substance, the most dependent part being occupied with a grey powdery pus. This has been attributed to its admixture with the pancreatic juice.

In the great majority of cases, inflammation appears to extend to the pancreas from neighbouring organs; in some cases it becomes adherent to the stomach at a point where the latter is undergoing perforative ulceration, and I have seen a case where this adhesion had a conservative effect and served as a stopgap, whereby, when the ulcer had completely eaten through the coats of the stomach, the escape of its contents into the abdominal cavity was prevented. Portal speaks of abscess in the pancreas having been frequently observed in disease of the testicles, and mentions one case in particular in which, after the extirpation of a testicle and the ligature of the spermatic cord, a large quantity of pus was found in the cord, and a considerable abscess surrounding the pancreas; and he refers to Antoine Petit as adducing different examples of this kind in support of his objections to the practice of ligature. M. Tonnellé mentions two cases of puerperal peritonitis in which pancreatic abscess occurred. In Mr. Lawrence's case the patient died five weeks after delivery. It is to be regretted that in these cases more accurate dissections were not made, particularly with the view of ascertaining the condition of the venous connexion between the parts primarily affected and the pancreas: it is very possible that the inferior mesenteric vein might have been found in a state of inflammation, and the pancreatic abscess might have been from secondary purulent deposit transmitted to it by branches from the splenic vein after the junction of the inferior mesenteric vein with it.

The contents of a pancreatic abscess may be discharged in various directions. Sometimes they escape into the cavity of the abdomen; sometimes they pass into the stomach, and sometimes into the duplicature of the mesocolon, where they may be retained as in a sac, or, having perforated one of its laminæ, may be effused into the general cavity of the abdomen. It is supposed also that the pus of a pancreatic abscess may find its way into the intestinal canal, and be discharged by stool without any obvious communication being established between them. Thus, in a case communicated by Dr. Haygarth to Dr. Percival, in which, on dissection after death, the pancreas was found to contain a considerable abscess, blood and, at length, fetid pus had been discharged by stool during life.

According to Dr. Pemberton*, ulceration is a very frequent result of inflammation of the pancreas; and from the small degree of sensibility with which the organ is endowed, the destruction may go a great way without pain or any symptom previously existing which could lead to a suspicion that inflammation was going on.

Portal alleges that gangrene of the pancreas is a *frequent* consequence of its inflammation, and that he has met with it in several instances. In one case, which he particularly specifies, the pancreas was found, on examination, to be of a violet purple colour, softened, and allowing a blackish fetid humour to exude from its external surface. "In short," he says, "it was gangrenous almost throughout its whole extent." Gendrin quotes what he conceives to have been a case of gangrene of the pancreas, occurring after chronic inflammation, and suggests it as probable that in this, as in other tissues, acute inflammation passes readily and completely into the state of sphacelus, only in cases in which the organ has been weakened by previous disease.

e. Hæmorrhage.—I have only met with two cases of hæmorrhage in the pancreas: one recorded by Mr. Fearnside, in which the right extremity was occupied by a large coagulum; the other related by Storck, in which the pancreas was so large and heavy that it exceeded thirteen pounds in weight. On cutting into this mass, it was found to consist merely of a sac filled with blood, partly grumous, partly coagulated, and beginning, it is stated, to become organised.

d. Structural changes. 1. *Non-malignant; cartilaginous transformation.*—Many cases are on record in which the pancreas had been found cartilaginous; it is generally enlarged, nodular on the surface, and very hard. In the majority of cases, one or more neighbouring organs have been found similarly affected; but in some rare cases the pancreas has been the exclusive seat of the cartilaginous degeneration. In persons affected with it nausea, vomiting, thirst, pain in the epigastrium, &c., had existed, and it was probably the remote consequence of chronic inflammation.

Steatomatous concretions. — Portal states that the pancreas is sometimes found full of steatomatous concretions, hard or softened, white like suet, or yellowish like honey. Sometimes the pancreas is enlarged by this matter throughout its whole substance, sometimes it exists only in particular parts. Those who have died of scrofula, and in whom the glands of the neck, axillæ, groins, or mesentery were obstructed, had likewise the pancreas equally affected. He mentions a particular case in which the mesenteric glands were full of steatomatous concretions, and in which the pancreas, besides being enormously enlarged and full of similar concretions, was covered by one of the consistence of suet and more than five or six lines in thickness. In this case the surrounding cellular texture, the mesocolon, and the parietes of the stomach, were cartilaginous and thickened, in consequence, he supposes, of the pressure of the tumour. He states, however, that the pancreas has been found affected when no marks of scrofula were observable in any other part of the body. Meckel states that he has seen the organ changed to an almost tophaceous mass.

The steatomatous concretion of Portal seems to be identical with the *tubercle* of the present day; and accordingly, both in the human subject and in the lower animals, tubercles of the pancreas have been occasionally met with, particularly in cases in which the lungs had undergone a similar degeneration. M. Lombard states that of one hundred cases of tuberculous disease in children which he examined, he found, in five, tubercles existing in the pancreas.*

Cystic tumours; hydatids. — These are of rare occurrence. M. Becourt has described a preparation in the Museum of the Medical School at Strasburg, of a cyst of very large size in the body of the viscus. Dr. Gross has given the following description of one, in a communication to the Medical Society of Boston.† On opening the body, a voluminous fluctuating tumour of oval form was found situated beneath the right lobe of the liver, with which it had contracted intimate adhesions. It was placed between the intestines and the posterior abdominal wall, passed a little to the left of the vertebral column, and had in front of it the curvature of the duodenum. It contained from 10 to 14 ounces of a sero-sanguinolent fluid without clot, slightly viscid, and without any appearance of fatty matter. There was not a trace in its walls of any of the normal tissue of the pancreas, although it was evidently formed by that organ. It contained some very small calculi, resembling those ordinarily met with in the ramifications of the pancreatic duct, and two of these, from three to four lines in dia-

* On Diseases of the Viscera, p. 63. et seq.

* Library of Medicine, vol. iv.

† Archiv. Gén. de Méd. iv. serie, t. 218.

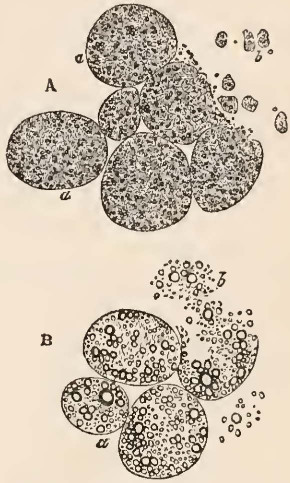
meter and rough on their surface, completely obliterated the opening of the pancreatic canal into the duodenum; they were composed of carbonate of lime. The rest of the pancreas — that is to say its left extremity — was about two inches long and very hard: *the pancreatic canal of this portion of the gland opened into the cavity of the cyst.* This circumstance, and the fact that that portion of the duct leading from the cyst to the duodenum was blocked up by the calculi, make it exceedingly probable that the cyst was primarily nothing but a dilatation of the duct in consequence of this obstruction. It is possible that this may be the origin of most of these cysts, and much to be regretted that the fluid contained in them has not been submitted to a rigorous examination, with the view of ascertaining whether it has any analogy to the secretion, or admixture with it. Two cases of retention of the pancreatic fluid recorded by Cruveilhier, confirm the probability of this supposition. "The dilated canal resembled a transparent cyst; the contained fluid was extremely viscid and clear, but of a whitish hue like a solution of gum arabic; it had a slightly saline taste; the collateral ducts were extremely dilated. There were some white patches, resembling plaster, in the centre of many of the lobules. This substance was more abundant in some of the lobules, and, when removed, presented the appearance of small lumps of plaster or chalk." These cretaceous lumps might have been of the nature of pancreatic calculus, which we have already seen associated with a cyst involving the duct, or the earthy remains of old tubercle.

Fatty degeneration. — I have frequently met with fatty degeneration of the pancreas, and all the instances in which I have detected it have been cases of *diabetes*. After finding it in four successive cases of this disease, I fancied that I had hit upon its cause and the secret of its true pathology. Although it seemed rather a "lucus a non lucendo" argument to attribute an undue formation of sugar to the derangement of a sugar-forming organ, yet in a class of bodies so full of instances of isomerism as the starch and sugar series, it appeared to me possible that an imperfect or depraved pancreatic secretion might give rise to the formation of an imperfect glucose incapable of those after changes by which it is worked out of the circulation. The meeting, however, with other cases of diabetes in which the pancreas was not fatty, and, still more, the perusal of M. Bernard's observations with regard to the part that the liver plays in the formation of sugar, and the disease of diabetes, dispelled my theory, and compelled me to regard the fatty state of the pancreas as the consequence, and not the cause, of the diseased condition, undergoing this degeneration in common with other organs; for I never found fat in the pancreas without finding it in enormous quantity in the liver and kidney. I may here remark, that I have not been able to confirm Dr. Johnson's observation*, that in diabetes, when the kidney cells contain a large quantity of oil, the hepatic cells contain an unusually small amount, and have a "starved" appearance; for I have invariably found the accumulation of fat in the liver and kidney cells, in cases of diabetes, in *direct*, and not in *inverse*, proportion.

* Diseases of the Kidney, p. 395.

The microscopical appearances of fatty pancreas are of two kinds, depending, I think, upon the length of time the degeneration has existed, and the amount of fat (*fig.* 75.). In one, the amount of fat is small, the globules very minute, confined to distinct epithelium cells,

Fig. 75.



Fatty Degeneration of the pancreas.

A. The process here is but slightly advanced, the oil-globules small, and the epithelium distinct, particularly where some cells have escaped, as at *b*; at *a*, too, within the follicles, they are visible.

B, another specimen, in which the fat was more abundant, and the destruction of the tissue complete.

and giving them, from the increased opacity it imparts to them, a more definite individuality (A. *a*.); in such a case, if a follicle is ruptured the epithelium escapes, each cell containing its own minute fat globules (A. B), and the amount of free fat, if any, is very small. In the other case, the appearance of individual epithelium cells in the follicle is altogether lost, the fat globules are larger and more numerous, and the rest of the contents indistinctly granular. (B. *a*.) Sometimes the oil globules completely fill the follicle; when in such a case pressure is applied, and the follicle contents forced out, no distinct epithelial cells are seen floating about, but all that is not fatty is amorphous and broken down. (B, *b*.)

2. *Malignant.* — *Scirrhus and carcinoma.* — These appear to be among the commonest affections of the pancreas. The disease generally affects, or commences in, a part only of the organ; and appears to be primarly pancreatic, for in some cases the pancreas alone has been found affected. Dr. Bigsby enume-

rates twenty-eight cases in which the disease appeared to be idiopathic, and in eight, which were of long standing, did not extend beyond the pancreas; more frequently, however, it implicates neighbouring parts in some degree, particularly the duodenum, stomach, and pylorus. It may exist without any increase of size, but more frequently is attended by some enlargement, which may be considerable. Scirrhus rarely goes on to ulceration, the associated lesions terminating fatally before that time. It often gives rise to constriction of the bile-duct and deep jaundice, and even compression of the aorta: this compression and constriction of the aorta have been known to occasion aneurismal dilatation above the seat of the constriction, as seen by Portal and Salmade.

Of the twenty-eight cases analysed by Dr. Bigsby, in seventeen the disease had not arrived at the stage of softening, although some of them had existed for years; it was purely scirrhus. In five cases he states the scirrhus had, at the time of death, passed into the soft state called *cephaloma* by Dr. Carswell, and *medullary sarcoma* by previous writers. Some parts, however, were as hard as cartilage; but others had all the pulpy, pale yellow, brain-like character of the second stage of scirrhus. In one case, the pancreas was changed into a sac, with a few shreds of cephaloma here and there on its sides. Lastly, in two cases no vestige of any form of scirrhus remained, the gland being altogether in a state of cancerous ulceration.

Fungo-hæmatoid disease has been found in the pancreas in three cases by Dr. Abercrombie, and in single instances by Dr. Bright and others. Dr. Copland found this lesion in the pancreas of a boy fourteen years of age; several other organs were also affectedby it.*

e. Calculous concretions in the pancreatic duct and its branches are by no means uncommon, and appear not unfrequently to be the cause of some of those morbid changes that have been already noticed. Sometimes they are manifestly in the duct; at others, though probably primarily so, they appear, from obliteration of the duct in which they were lodged, to be in the gland substance. They are usually white, but occasionally black; they vary much in shape, being sometimes round, and sometimes irregular; their size ranges from that of a pea to that of a small walnut, and their number from one to twenty; sometimes they are scattered throughout the gland, sometimes aggregated in a mass. Gendrin mentions that the pancreatic duct is sometimes clogged, not with distinct concretions, but with a chalky powder. In respect to chemical composition it seems probable that pancreatic calculi are liable to some variations. Dr. Pemberton† mentions having received one from Dr. Baillie from the human pancreas which consisted entirely of carbonate of lime; whereas, one from the ox analysed by Dr. Wollaston turned out to be phosphate of lime. Portal mentions that in a case in which he met with a dozen of light, round, whitish calculi in the pancreas, he found that when he reduced one or two to coarse powder, and threw this into boiling water, it readily dissolved; and Fourcroy states, as the result of his examinations, that pancreatic concretions are composed of phosphate of lime combined with some animal matter, just as is the case with salivary calculi.

* Medical Dict. Loc. cit.

† On the Viscera, p. 68.

There is one circumstance connected with the morbid anatomy of the pancreas worthy of special note, and with a short reference to this I shall finish this paper; it is

The occurrence of fatty stools in connection with pancreatic disease. Attention was first drawn to this subject twenty years ago by the simultaneous publication, in the eighteenth volume of the Medico-Chirurgical Transactions, of papers by Drs. Bright and Elliotson and Mr. Lloyd; but although the subject excited considerable interest at the time, it has since been suffered to lapse, from want apparently of due appreciation of its import; and it is only recently that it has emerged from its obscurity in consequence of the new interest with which recent physiological discoveries have invested it. It is only the most hasty and superficial glance that it will be possible here to give to this most interesting subject: for further details I must refer the reader to the original papers, to others that have since been published, and to an admirable article in the twenty-third number of the British and Foreign Medico-Chirurgical Review.

The first of these papers — first as much in importance as in time — was that of Dr. Bright. Not only was he the first to point out the pathological relations of this remarkable phenomenon, but his paper is distinguished by a singular clearness and impartiality, and by a thorough digestion of its carefully gathered materials. He thus describes the peculiar condition of the evacuations that first excited his attention: — "A portion more or less considerable assumes the character of an oily substance resembling fat, which either passes separately from the bowels, or soon divides itself from the general mass, and lies upon the surface, sometimes forming a thick crust, particularly about the edges of the vessel, if the fæces are of a semifluid consistence; sometimes floating like globules of tallow which have melted and become cold; and sometimes assuming the form of a thin fatty pellicle over the whole, or over the more fluid parts in which the more solid figured fæces are deposited. This oily matter has generally a slight yellow tinge, and a most disgustingly fœtid odour."

After detailing the cases, Dr. Bright institutes the following analysis of them:—"In all of these, chronic ailments terminated, sooner or later, in jaundice; and in all of them a great peculiarity in the character of the dejections existed. In the result of the examination after death we have likewise some circumstances which coincide in all — *obstructed* *biliary ducts; the liver gorged with bile; fungoid* disease attacking the *head of the pancreas;* and *malignant ulceration* on the surface of the *duodenum.* The question to be solved is, upon which of the conditions indicated or caused by these morbid changes, if upon either, the peculiarity of the alvine evacuations depended? That the obstruction of the biliary ducts, or even the total absence of all indication of biliary secretion, is not usually attended by the same peculiarity in the evacuations, many cases which have been cautiously detailed by various authors, and many which we have all observed, bear sufficient testimony; and I was therefore induced to ascribe it, either to the existence of malignant disease, or to that disease being situated in the pancreas. That the simple fact of malignant disease existing is not *necessarily* productive of such appearances in the fæculent matter, I infer from cases both of that form of disease and of melanosis in the liver to a very great extent being, within the scope of my experience, unaccompanied by any such discharge, though the evacuations were submitted to the most rigid observation. That simple ulceration in the bowels to any known extent, is not attended by any such symptom I am led to believe from knowing that neither in the most extensive ulceration of the large intestines in cases of dysentery, nor in the worst cases of ulceration of the small intestines in fever, in diarrhœa, or in phthisis, does anything of the kind occur. Whether, however, malignant ulceration of the mucous membrane is accompanied by this symptom I cannot assert, though I have often seen most extensive ulcers of the pylorus and of the rectum, where, although the evacuations were attentively observed, such fatty matter was not detected. As, however, a malignant ulceration of membrane did exist in each of the foregoing cases, it is not impossible that this was the cause of this symptom; but we must bear in mind that such ulcerations are *by no means* uncommon, and that the phenomenon of which I am speaking *is* uncommon; and that in each of the cases it was accompanied by another morbid appearance, which is not common; namely, the malignant disease of the pancreas. The fact of the intestinal ulceration having in each case occupied the duodenum does, however, somewhat diminish the weight of this observation, for that certainly is not so frequent an occurrence." By this process of elimination, and by the instance of other cases more or less analogous, Dr. Bright conceives that we may bring the circumstances of the diseased structure in connection with this symptom within a narrow limit — "*disease, probably malignant, of that part of the pancreas which is near the duodenum; and ulceration of the duodenum itself.*" To this conclusion, however, so carefully arrived at, subsequent observation has shown that exception must be taken: cases that have occurred since the publication of Dr. Bright's paper, and even quite recently, have proved that neither the malignant character of the disease nor ulceration of the duodenum is necessary to the production of the fatty stools. In a case in which fatty stools occurred, communicated to the Society of Medicine of Boston*, in one reported by Dr. Alfred Clarke, of Twickenham, in the Lancet for August 16. 1851, and in one referred to by Dr. Kirkes in his Handbook of Physiology†, the pancreatic disease appears to have been clearly non-malignant, and to have consisted in the conversion of the organ into a serous cyst in consequence of obstruction of its duct; and the duodenum seems to have been quite healthy. In two, however, of these cases, there was jaundice, and in the third deficient bile in the evacuations, so that the pancreatic disease was not *pure.* What we want for the clearing up of this subject as far as the pancreas is concerned is, a case in which the pancreas *alone* is affected, other organs not being even functionally implicated, and in which there is during life a clear presence, or a clear absence of fatty stools. Until such a case or cases can be brought forward, the light which this section of pathology has thrown upon physiology will still leave undetermined the relative importance, in effecting the absorption of fat, of the different digesting agents supplied by or poured into the duodenum.

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* Archiv. Gén. de Méd. t. xix. p. 215.
† P. 233.

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(*Hyde Salter.*)

PELVIS. (πελυξ, Gr.; *Pelvis*, Lat.; *le Bassin*, Fr.; *das Becken*, Germ.) — The pelvis is the bony girdle which connects the spinal column with the bones of the lower or hinder extremities.

It derives its name from its supposed resemblance in the human subject to a basin. Its figure, however, varies greatly in different animals. The description which follows, refers to the *human male pelvis*, which may be taken as a standard of comparison. It is composed of three principal pieces, two of which are symmetrical in shape, lateral in position, connected anteriorly, and called the *innominate* bones; and the third, called the *sacrum*, intervenes between the former at their posterior extremities, and connects them to the spinal column, of which it forms the inferior or posterior portion. Appended to the lower extremity of the sacrum is a small bone, the *coccyx*, — the representative of the caudal bones in the lower animals, — which, as influencing the shape and completing the formation of the walls of the pelvis, is considered as a part of it.

The Innominate Bone (*Os innominatum, coxarum, sive pelvis lateralis*, Lat; *l'Os d'ile, coxaux*, Fr.; *das ungenannte Bein*, Germ.; — *figs.* 76, 77.) is a bone of so irregular a shape as to leave it without a name in the fanciful nomenclature of the older anatomists. It is broad and expanded at the upper extremity, rounded and perforated at the lower, constricted in the middle like a figure of 8, and bent into a curve, with its concavity directed forwards, upwards, and inwards, at the upper end; and backwards and inwards at the lower, so as to form a segment of the pelvic circle.

Its *office* is to support the bones of the lower extremities; to transmit to them from the sacrum the weight of the trunk in the erect position; and to afford a basis of support in the sitting posture. It also forms a protecting enclosure to the important viscera within it, and gives attachment to the abdominal and leg muscles.

This bone is usually described in three separate portions, into which it is separable in young persons, and which are called, respectively, the *haunch bone* or *ilium* (*das Hüftbein*, Germ.; *l'Ileon*, Fr.); *the seat bone* or *ischium* (το ισχιον, Gr.; *das Sitzbein*, Germ.; *l'Ischeon*, Fr.); and the *share bone* or *pubis* (ὁ κτεις, Gr.; *das Schaambein* or *Schoossbein*, Germ.).

Of these three, the ilium forms the upper expanded portion, and the pubes and ischium the lower perforated portion; the former being placed before, and the latter behind the opening. In the perfect bone, however, these three are completely soldered together by bony union in the central constricted portion, where each contributes to form a deep cavity, externally, for the reception of the head of the thigh bone. From this cavity the three portions radiate; the ilium upwards, the ischium downwards, and the pubes forwards, each contributing to support the thigh bone by its central extremity. The innominate bone may, however, be most briefly described as one bone, consisting of two *surfaces*, *external* and *internal*; bounded by four *borders*, *superior*, *inferior*, *anterior*, and *posterior*.

The *superior border*, formed entirely by the ilium, is the most regular and the most extended. It forms an arch, directed from behind forwards and outwards, and curved laterally so as to present, on looking at it from above, the shape of an italic *f*; the smaller concavity being posterior and directed outwards; and the larger, anterior and directed inwards, contributing to form the general concavity of the internal surface. This border is thickened in a somewhat irregular manner, forming what is called the *crest of the ilium* (*a*, *c*, *b*), upon which may be traced an *internal* and an *external lip*, and a rough broad *central line*. These ridges are caused by the attachment of the abdominal muscles. The external lip is called, by some authors, *the superior curved line* of the ilium. The crest is very much thickened and irregular at the posterior extremity, where it terminates in a backward projection, the *posterior superior spinous process* (*b*). It is also thickened into an outward projection a little in front of the centre (*c*), and also in a less degree at the anterior extremity, where it projects forwards, forming the *anterior superior spinous process* (*a*).

The *anterior border* consists of an upper vertical portion formed by the ilium, and a lower oblique portion formed by the pubis. It commences above at the anterior superior spine, an inch below which it presents a similar projection called the *anterior inferior spinous process* (*d*), the two being separated by a smoothly edged *notch* (*u*). Below the inferior spine is another indentation, wider and less deeply marked, and forming part of the overhanging edge of the cavity for the thigh bone, and in which a muscle lies. To this succeeds below, another rounded, less strongly marked prominence, in which the ilium and pubes are united, called the *ilio-pectineal eminence* (*e*). From this point commences the oblique or inward direction of this border, which is for about two inches smooth and rounded for a muscle to glide over, and then presents a fourth well marked, acute, forward projection called the *spine of the pubis* (*f*), which is continued by a rough strongly marked ridge, the *crest of the pubis* (*f, g*), to the termination of this border in an abrupt right angle, the *angle of the pubis* (*g*). All these eminences result from the implantation of the tendons of muscles of the leg or abdomen.

The *inferior border*, composed partly by the pubis, but principally by the ischium, here commences. It is arranged first in a rough, indented, plane, oval, and vertical surface, which in the living bone is united by fibro-cartilage to innominate bone of the opposite side, and forms the *symphysis of the pubis*;—συμφυμι, to grow together (*h*). The posterior border of this articular surface is often raised into a ridge, projecting backwards, especially in old persons. Cruveilhier mentions one, observed in a woman who had borne many children, where this was a perfect crest. Below this point the border assumes a direction tending first downwards and outwards, and then, somewhat sharply, curving upwards and backwards. Just below the symphysis it presents a sharp, rough, irregular ridge, with a considerable outward eversion, affording attachment to strong fasciæ and muscles of the leg and perineum, and to the root of the penis. At the most depending part it gradually widens into a very rough, large, elongated, and rounded tuberosity, 3 inches long by 1½ broad at its posterior extremity, the *tuberosity of the ischium* (*i*). This tuberosity has a general inclination outward; and along its inner margin, which projects lower than the outer, is a raised ridge for the attachment of the great sciatic ligament. Upon it are implanted the large posterior leg muscles, and in the sedentary position the trunk is supported by it. Hence the name of this portion of bone (from ισχειν καθημενος—quod sustineat sedentes), and also its German appellation (Sitzbein or Sitzstück).

The *posterior border* commences above this tuberosity. Its direction is first vertical, and then irregularly horizontal. It is formed by the ischium and ilium. Above the tuberosity of the ischium is a rounded groove, in the fresh state covered by cartilage, and called the *small sciatic* or *obturator notch* (*k*), over which a muscle glides. Then occurs a sharp prominent process, turned considerably inwards, giving attachment to a strong ligament and some muscles, and called the *spine of the ischium* (*l*). Above this the border is thin, rounded and vertical, becoming gradually much thicker and finally curving sharply backwards and downwards. It thus forms a large *notch*, the *great sciatic*, formed principally by the ilium (*m*). To this succeeds a tapering, elongated, and depending prominence called the *posterior inferior spinous process of the ilium* (*n*), serving for the attachment of ligaments. The border then presents an insignificant rounded notch, with a thin edge; and finally terminates in the superior border at the *posterior superior iliac spine*, already described.

Fig. 76.

External view of the innominate bone.

The *external* or *femoral surface* of the os innominatum (*fig.* 76.) at its upper or iliac portion is directed outwards, backwards, and slightly downwards; at its central part outwards; while its pubic and ischiatic or lower part is directed forwards, downwards, and outwards. The iliac portion is broad and fan-shaped above, whence this upper portion is called the *ala* or *wing of the ilium*. It is convex at its anterior, and concave at its posterior portion, following the *ʃ* curve of the crest before mentioned. The concavity is termed by many writers the *external iliac fossa*. The convexity is increased by a ridge of thick bone, which passes vertically downwards from the thickened portion of the crest to the cavity for the thigh bone. At the posterior part of this surface, close to the termination of the crest, is an elongated rough impression of a somewhat triangular shape, having its base at the superior and inferior posterior spines, and tapering off gradually along the crest for about three inches, which marks the origin of a great muscle—the gluteus maximus, and which may be called the *gluteal impression* (1). In the middle of this surface is a slightly marked line of an irregular curvature, commencing posteriorly at the centre of the great sciatic notch, and, passing upwards and forwards, terminates in the crest a little posterior to the anterior superior spine. This is the *superior curved line* (2) — (*posterior* of Cruveilhier). Below this is another line of a like character, the *inferior curved line* (3) — (the *anterior* of Cruveilhier); which, commencing an inch below the other in the sciatic notch, gradually diverges from it, and terminates anteriorly at the inferior spinous process of the ilium. The surface presents numerous small circular openings for the admission of the nutritious vessels of the bone, all of which have a direction downwards towards the articular surfaces.

About an inch and a half below the inferior curved line is a large articular cavity for the reception of the head of the thigh bone, which is named the *acetabulum*, or *cotyloid cavity*,— κοτυλη, a cup; and εἶδος, like (4). This is a perfectly hemispherical excavation of about two inches diameter in the full grown male, and circumscribed by a rough irregularly raised *brim* or *circular border*, to which is attached the circumferential fibro-cartilage or cotyloid ligament of the hip-joint. When the bone is properly placed, as in the articulated skeleton, the axis of this cavity is directed outwards and a little downwards for the better adaptation of the femur; and to this end the posterior part of its circumference is much thicker and more prominently elevated than the anterior. Superiorly it is still more evidently prolonged outwards at the point where the before mentioned thick vertical ridge of the ilium springs from it. Inferiorly the border is interrupted for the space of an inch by the *cotyloid notch* (5), to the edges of which are attached the transverse and interarticular ligaments of the hip-joint, and which is continued into the centre of the cavity by a rough *depression* or *fossa*, for the reception of some lubricating glands and the interarticular ligament connected with the femur. The bottom of the notch is on the same plane as that of the depression, and affords an entrance for the vessels and nerves supplying the joints. The remainder of the cavity is a smooth and even *surface*, uniformly concave and circular, which is covered in the fresh state by a cartilage of a semilunar shape. The broadest part of this surface is above where the superior border projects. The posterior extremity is prolonged into a lip which a little overhangs the notch posteriorly, and terminates exactly opposite to the broadest part of the overhanging superior margin. The anterior extremity is the narrowest, being notched slightly by the groove below the anterior inferior iliac spine on the anterior border of the bone before mentioned. At the bottom of the cotyloid fossa may be traced two lines arranged in the shape of a T, the lower limb of which divides the cotyloid notch into nearly equal portions. These mark the fœtal division of the bone into three portions, of which the ilium contributes the two superior fifths, the ischium the inferior posterior two fifths, and the pubis the remaining anterior inferior fifth, to the formation of the cotyloid cavity. Externally, the *brim of the acetabulum* is convex, rounded, rough, and marked above and behind by the attachment of the capsular ligament of the hip-joint (6). It is here perforated by numerous foramina for the admission of nutritive vessels. It is much better pronounced above and behind, where it presents a broad, thick, convex surface, than in front where it is shallow, thin, and slightly depressed. The points where this difference is indicated are, the inferior spine of the ilium above, and the cotyloid notch below.

Springing from the cotyloid cavity are two branches of bone; one from the inferior part, thick, massive, directed downwards and backwards called the *descending ramus* or *body of the ischium* (*p*); and the other, from the anterior part, slighter in structure, and directed obliquely downwards, forwards, and inwards in the same plane with the ilium, called the *horizontal ramus* or *body of the pubis* (*q*). These are each prolonged at their further extremities into flattened tapering processes, which, altering the original direction of their respective portions of bone, one ascends obliquely inwards, and the other descends obliquely outwards, to unite with each other midway, at a point marked by a slight transverse line. They are named respectively the *ascending ramus of the ischium* (*r*), and the *descending ramus of the pubis* (*s*).* Together they form the inferior border of the innominate bone, and complete the formation of a large oval opening, situated immediately below, and a little internal to the cotyloid cavity, having its long axis directed obliquely downwards and outwards, and called the *obturator* or *thyroid foramen* (*o*) — θυρεος, a shield; and εἶδος, like. The edges of this opening are thin, bevilled off, and rough, for the attachment of a fascial ligament which closes the opening, and are formed entirely by the ischium and pubes. The external edge, instead of meeting the internal superiorly, is continued inwards in front of it, along the superior ramus to the spine of the pubes before described, forming a prominent rib of bone of a triangular shape (*q*), its base abutting on the cotyloid cavity. This rib is convex vertically, and concave laterally. Between it and the internal edge of the thyroid foramen is left a groove, called the *sub-pubic or obturator groove* (*t*), for the passage of a nerve and vessels, and which has a direction downwards and inwards. The junction of the horizontal and descending rami of the pubis is called the *angle of the pubis*, and it is hol-

* There has been much confusion in the application of names to these bones, the term *body* of the pubis is applied by some to the *angle*, and by others to the cotyloid portion only. The term *body* is confined also by some to the acetabular part of the ischium. The expressions *horizontal* and *descending* rami of the pubis and *ascending* ramus of the ischium were applied before a true knowledge of the pelvic obliquity was obtained. The former would probably be well superseded by the words *superior* and *inferior*, and those applied to the ischial rami by *anterior* and *posterior*, or *greater* and *lesser*.

lowed, rough, and broad in front, for the attachment of some muscles of the leg. There are numerous nutritious openings on this surface of the ischium and pubis, which are chiefly directed *towards* the cotyloid cavity.

Fig. 77.

Internal view of the os innominatum.

The *internal* or *pelvic surface* presents for examination a superior or iliac portion directed forwards, upwards, and inwards, and an inferior ischio-pubic portion directed inwards and backwards.

The iliac portion is rough at the posterior third, and is marked by a thick, massy, irregular prominence, just below the posterior extremity of the crest, which is continued to the posterior superior spine, and serves for the attachment of powerful ligaments which connect this bone to the sacrum. This may be called, for brevity, the *iliac tuberosity* (1).

An inch and a half below this is an angular or semilunar *articular surface*, the *sacral*, or *auricular* (2), to which the sacrum is attached in the complete pelvis. This surface is generally more or less rough and irregular, for the more firm attachment of the articular cartilage. It is composed of two elongated portions placed at right angles to each other, of which the inferior is the longer, and is directed horizontally backwards to the posterior inferior spine, parallel with and close above the upper boundary of the great sciatic notch (*m*, *n*), while the superior is directed vertically upwards towards the crest of the ilium, to which its raised anterior border is prolonged by a well marked ridge (3). At the angle of junction of these two limbs is generally to be seen a deep hollow, while the extremity of the inferior limb is bevelled off to correspond to elevations on the opposed surfaces of the sacrum. In the retiring angle formed by the auricular surface is a very rough depression for the attachment of inter-osseous ligaments (7).

The anterior two thirds of the internal iliac surface forms a complete smooth and regular hollow called the *internal iliac fossa* (4) for the reception of a muscle, which is continued downwards and forwards into the groove before described, below the anterior inferior spine of the ilium (*d* to *e*). At a small distance in front of the articular surface, is a large nutritious opening, directed downwards and forwards towards the cotyloid cavity, for the passage of the principal nutritive artery of this bone. Many others of less calibre, all directed downwards, also exist on this surface. Passing downwards and forwards from the angle of the sacro-iliac articular surface is a thick, rounded and arched ridge of bone (5), which serves to transmit the weight of the spine from the sacral articular surface to the femur at the cotyloid articulation. Just behind the ilio-pectineal eminence, before described, this line becomes more salient, and passes from this point to the spine of the pubes as a well marked projecting crest, the *ilio-pectineal line* (6), which serves for the attachment of a muscle of the leg, and some strong fasciæ. The internal surface of the pubis and ischium, and the small inferior, or true pelvic portion of the ilium, are seen below this line, which separates them from the iliac fossa. Posteriorly is seen a broad, flat surface (*p*), to which is opposed the cotyloid cavity externally, and the rough lines, marking the junction of the three component bones, are repeated more strongly and more extensively here than in the cotyloid cavity itself. They form a Y shape, the posterior limb of which is directed backward to the top of the great sciatic notch; one branch terminates at the pectineal eminence; and the other at the obturator opening, where it passes into the commencement of the subpubic groove (*t*), the termination of which was described with the external surface. Anteriorly is seen the inner aspect of the obturator foramen (*o*), and the posterior surfaces, and slightly marked line of union of the branches of the pubis and ischium (*r*, *s*), which are smooth, rounded off, and laterally convex for the apposition of the pelvic viscera. Below is the inner aspect of the great tuberosity of the ischium (*i*), which is also smooth and concave for the like purposes.

Internal structure of the innominate bone. — Like other irregular bones, the haunch-bone is composed of cancellous structure, encased in layers of laminated bone, more or less thick, as strength and tenacity are required. The thickest and strongest part of the haunch-bone is the arched, rounded rib, extending from the cotyloid cavity to the auricular surface and tuberosity of the ilium, which is the direct line of pressure from the spine to the legs. A cross section of this part of the bone is nearly an inch in diameter, generally, at its narrowest point. The descending rami of the ischia are the next in point of strength, for supporting the body in the sitting posture. These parts are composed chiefly of hard, laminated bone of dense section. The crest of the ilium is of a spongy structure, as also are the thick masses of bone at the tuberosities of the ilium and ischium, and around the cotyloid cavity. The thinnest parts of the bone are at the bottom of this cavity, and in the centre of the iliac fossa, at which places is so little cancellous structure, that the thin laminæ, forming the whole exterior of the bone, meet each other, and are so thin as to be sometimes translucent.

The Sacrum (Syn. *το ιερον*, Gr.; *Os sacrum, basilare*, Lat.; *l'Os sacrum*, Fr.; *das heilige*, or *Kreuz Bein*, Germ.) is a single pyramidal bone, flattened antero-posteriorly, and placed in the median line, with the apex downwards, the anterior aspect being directed downwards and forwards, and the posterior upwards and backwards.

Its *office* is to form a basis of support to the spinal column and its appendages, and, acting like the keystone of an arch between the haunch-bones, to transmit to them its superincumbent weight. It also encloses and protects the terminal divisions of the spinal cord, and transmits them to the inferior parts of the body, and it completes the pelvic cavity behind, and affords attachments to the strong muscles of the back. It presents for examination four *surfaces; anterior, posterior*, and *lateral*, a *base* and an *apex*.

The *base* (*fig.* 78. A) is directed forwards and upwards, and has a general resemblance to the upper surface of a vertebra, the lateral parts exactly corresponding to each other, as in most single bones. In the centre, anteriorly, is a large, plane, oval, articular *surface* (1) for fibro-cartilaginous union with the last lumbar vertebra, of which the long diameter is placed transversely, and about two inches long. On each side of this surface extends a large, fan-shaped, flattish mass of bone (2), spreading externally, with a rounded anterior border, arching laterally, and forming part of the brim of the true pelvis. On the posterior border is seen a rounded prominence. At the junction of the lateral masses with the oval articular surface posteriorly, two *articular processes* (*a, a′*) project upwards and backwards to articulate with those of the last lumbar vertebra. Their roots are marked anteriorly by deep grooves, in which lay the last lumbar nerves. Their *articular facets* are slightly concave, circular, vertically placed, and directed backwards and inwards, and receive between them their counterparts on the last lumbar vertebra. Springing from the roots of these processes, two long *laminæ* (1 B) pass backward and inwards with much downward inclination to meet each other in a stunted median *spinous process* (2 B), the commencement of the sacral crest. They correspond to the laminæ and spines of the true vertebræ. The *foramen* (3 B) enclosed by them is triangular in shape, and of considerable size, and is the superior opening of the *sacral canal*.

The *apex* (3 A) is a small oval, horizontal articular surface placed in the median line, with its long diameter half an inch in extent, and directed transversely. To it is articulated the base of the coccyx.

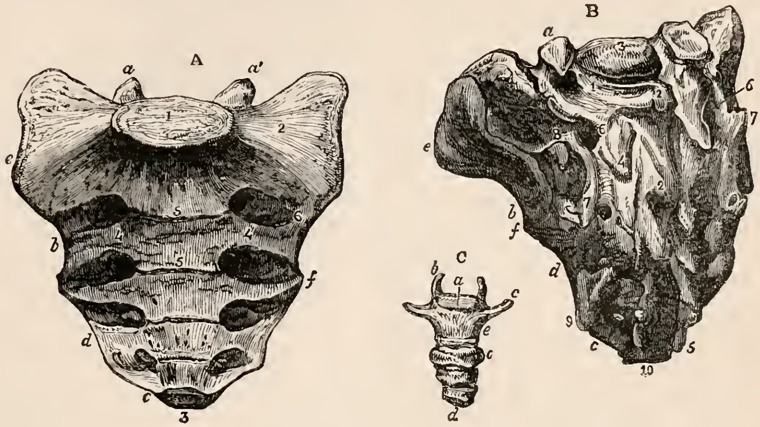
The *anterior* or *pelvic surface* is smooth and directed forwards and downwards, forming the posterior wall of the true pelvis. It is widest above, opposite the lateral masses of the base (*e*). A little below this point it is about three-fourths of an inch narrower (*b*). It then widens again to the extent of nearly half an inch (*f*), and then gradually tapers to the apex. It is considerably arched from side to side, especially at its superior part, where it has a transverse curvature, varying from half to three quarters of an inch in central altitude. Longitudinally, also, this surface is curved to a still greater degree, and with greater variations, upon the comparative extent of which, in male and female, anatomists are much disagreed.

On each side of the median line are four holes, the *anterior sacral foramina*, separated from each other by three rounded *transverse processes* of bone about half an inch wide (4), and placed at equal distances of rather more than half an inch from the median line. The two upper holes are of equal size, and much larger than the two lower. Each is connected to its fellow on the opposite side by four raised *transverse lines* (5), which mark the fœtal separation of this bone into five vertebræ; and extending outwards and downwards from each hole is a *groove* continued obliquely downwards to the borders of the bone (6). Below the last sacral hole, on each side, is a shallow notch, in the outline of the bone (*c, c′*), which is transformed into a foramen by the attachment of the upper transverse tubercles of the coccyx. There are many openings for nutritive arteries in this surface, directed generally towards the centre of the bone.

The *posterior surface* (*fig.* B) is rough for muscular attachments, and directed upwards and backwards. It is narrower than the opposing parts of the anterior at the upper part of the bone generally, by rather more than half an inch. According to Mr. Ward, a transverse section of the sacrum, an inch below the base (at the second sacral vertebra), shows that in this place the posterior surface is *wider* than the anterior by three sixteenths of an inch, so that the sacral wedge is here *reversed* in obliquity, which he considers of importance in resisting anterior dislocation of the sacrum. Above this point, the anterior surface is three sixteenths of an inch wider, and below, it resumes its superiority in width by four sixteenths. In some cases the back and front are of equal width; in others the anterior diameter exceeds the posterior throughout.

Its general curvatures are convex, following the concavities of the anterior surface. In the median line are four spinous processes (2), the first of which has been described with the base, connected by a sharp vertical ridge of bone, and corresponding to the four upper pieces or vertebræ of which the sacrum is composed, the whole being called the *sacral crest*. The last of these, and sometimes the two lower are divided by a *notch* (10), which opens u

Fig. 78.



A, *anterior surface and base of sacrum;* B, *lateral and posterior view of the same bone;* C, *anterior surface and base of coccyx.*

the *sacral canal* at its inferior termination, where it is much compressed antero-posteriorly. On each side of the sacral crest is a narrow vertical groove, corresponding to the vertebral laminæ, and bounded externally by four rough *tubercles*, the *articular* (4), the last of which are confounded with the bifurcated inferior spine, and project downwards in two *inferior sacral horns* (5), which are smoothed into facets posteriorly, to articulate with the coccyx. They correspond to the articular processes of the vertebræ. Immediately external to them, and on the same level, are the four *posterior sacral foramina* (6), of irregular size, but much smaller than the anterior, to which they are opposed in situation. The broad surfaces of bone between them present another continuous shallow vertical groove, external to which are three or four *tubercles*, the *transverse* (7), arranged vertically parallel with the holes, and corresponding to the tips of the transverse processes of the vertebræ. The highest of these are sometimes smoothed into a facet externally (8), by impinging upon the iliac tuberosity, and the *fourth* (9) is always *the largest and most prominent* for the attachment of the superficial posterior sacro-iliac ligaments. Close to the lateral boundary, opposite the two upper transverse tubercles, are two very rough, digital impressions for the insertion of powerful posterior sacro-iliac ligaments.

The *lateral surfaces* of the sacrum (*fig.* B) are broad above, and taper gradually downwards. When opposite the two last sacral vertebræ, they become narrow borders (*d*). Above, at the three upper vertebræ, they oppose the inner surface of the ilia — below, they form the inner margin of the great sciatic notch. At the upper broader portion these surfaces are bevelled off posteriorly, the posterior surface of the bone being at this part narrower than the anterior, and its plane being less distinctly different from that of the lateral surfaces. It is overhung by the tuberosities of the ilia. Close to the upper and anterior margins, occupying the two anterior thirds of the lateral aspect of the base, and extending as far downwards as the third sacral vertebra, at which point the anterior surface of the sacrum becomes, as before mentioned, broader, is a large, angular *articular surface*, the *iliac* or *auricular* (*e*), depressed along the centre, and exactly corresponding to the shape and irregular surface of the opposing articular surface of the ilium with which this bone is here jointed. The salient angle corresponds to the rounded anterior border of the lateral masses of the base, and the retiring angle, to the digital depression at the edge of the posterior surface. Two prominent portions may be particularly observed on this articular facet, one at the salient angle (*e*) on the first sacral vertebra, and another at the termination of the inferior limb (*f*) on the third sacral vertebra. They correspond to similar depressions in the opposed ilium.

The sacrum is traversed longitudinally down the middle, but nearer to the posterior than to the anterior surface, by the inferior termination of the *spinal canal*, which communicates with the anterior and posterior sacral foramina, the terminal nerves of the *cauda equina* being contained and distributed within it.

Internal structure of the sacrum. — The interior is composed of a closely reticulated mass of spongy bone, enclosed in thin, laminated surfaces. For its size, it is the lightest bone in the body, from being made up chiefly of cancellous structure. The laminæ, spines, and articular processes are, however, chiefly composed of dense bone.

The Coccyx (*fig.* c), the *huckle*, or *whistle* bone (named from its supposed resemblance to a cuckoo's bill, from κοκκυξ, Gr.; *Os coccygis*, Lat.; *l'Os coccyx*, Fr.; *das Steissbein*, or *Schwanzbein*, Germ.), is an appendage to the apex of the sacrum, and terminates the spinal column inferiorly.

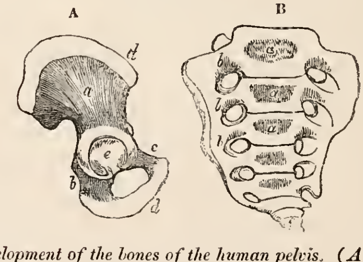
It forms the posterior boundary of the lower part of the cavity, and inferior outlet of the pelvis, assisting to complete its walls, to sustain its contents, and to attach some muscles of the leg and perineum. Its position is oblique from behind, forwards and downwards, but being normally movable on the sacrum, it yields to pressure in both ways. It is usually composed of four, rarely five pieces or tubercles, which are generally, but not always, soldered to each other, and diminished in size and completeness downwards. When in one piece, it presents a tapering, elongated, knobbed appearance with an *anterior* and *posterior surface*, two *lateral borders*, and a *base* and *apex*. The *base* presents a plane, oval, articular surface (*a*), corresponding to the apex of the sacrum, with which it is articulated, and sometimes ankylosed. Behind this, on each side, projects upwards and backwards a cornuated process (*b*), tipped with an elliptical articular facet, directed upwards and forwards, to articulate with the inferior sacral horns. Below these, the *borders* commence, presenting three alternate notches (*e*), and tubercular projections (*c*), of which the first are much the largest, and complete the sacro-coccygeal foramina. The borders are terminated by a knobbed, sometimes bifurcated *apex*, and give attachment to the sciatic ligaments, and some muscles (*d*). The first two of these notches are converted into holes by ligaments, for the passage of the posterior branches of the fifth and sixth sacral nerves. The *anterior surface* is slightly concave longitudinally, and smooth, to support the rectum. It has transverse markings, similar to the sacrum. The *posterior surface* is correspondingly converse and rough, to attach ligaments and muscles. The internal structure of this bone closely resembles that of the sacrum.

Developement. — The *innominate bone* is developed by *three* primitive and *five* complementary points of ossification.

The three *primitive* points commence in the three component parts of the bone, the ilium, ischium, and pubis respectively, from a single piece of cartilage of the general form of the bone. That of the *ilium* is placed in the thick, arched rib above the cotyloid cavity, (*fig.* 79. A, *a*), being apparent, according to Cruveilhier, the first in order, about the fiftieth day of fœtal life. Bischoff, however, says that the time of its appearance varies from the second to the fourth month, in different individuals. About the fifth month, it acquires somewhat of the form of the complete bone. That of the *ischium* is placed in the upper part of the descending ramus (*b*), and appears second in order of time, always later than the ilium, about the end of the third month, or, according to Bischoff, the fifth month. That of the *pubis* appears in the superior branch, near the ilio-pectineal eminence (*c*), at the end of the fifth month. Bischoff fixes it later than Cruveilhier, at the sixth or seventh month. At the period of birth, the cotyloid cavity is still principally cartilaginous (*e*), the ascending branch of the ischium, the descending of the pubis, and nearly the whole circumference of the ilium, still remaining in the same condition (*d*).

At the age of six or seven years, the branches of the ischium and pubis are united by bone. About the time of puberty, as first pointed out by M. Serres, a distinct *complementary* point of ossification appears in the cartilage dividing the bones in the cotyloid cavity, which soon including the whole of the Y-shaped cartilage at this part, and assuming its shape and serrated margins, finally unites them in the raised line before described. According to Meckel, the pubis and ischium join first with each other, and the ilium becomes united to them afterwards. At the same time appear the four remaining *complementary* points as epiphyses, in the following order: namely, 1. On the whole length of the iliac crest; 2. At the anterior inferior spine, not constant, and said to be more frequent in the male than the female; 3. Along the whole extent of the tuberosity of the ischium; 4. On the symphysial surface of the pubis, said by Beclard to be more often found in the female. All these are soldered to the bone, about the twenty-fourth or twenty-fifth year, the epiphysis of the iliac crest being the last to join.

Fig. 79.



Development of the bones of the human pelvis. (*After Quain and Sharpey.*)

A. Innominate bone of a full-grown fœtus; *a*, primary ossific point of ilium; *b*, do. of ischium; *c*, do. of pubis; *d*, *d*, cartilage; *e*, Y-shaped central cartilage.

B, sacrum and coccyx at birth; *a*, central ossific points; *b*, characteristic sacral do.; *c*, coccyx still cartilaginous.

The *sacrum* is produced by the soldering together of five vertebræ. Hence they have been called the *false* or *sacral vertebræ*. Occasionally six pieces have been found, and, more rarely, according to Sœmmerring, four pieces only are present. Each of these five pieces, as in the other vertebræ, results from three *primary* points of ossification, viz., one for each body or central portion, and two for the posterior lateral surfaces and laminæ of each vertebra. These appear later than in the true vertebræ, and are first manifest in the bodies of the three upper (*fig.* B, *a*), at the second or third month of fœtal life, and in the two lower at the fourth or fifth month. The lateral points are developed between the sixth and ninth fœtal months, and are united to the bodies (each after joining with its fellow opposite at the spinous tubercle) at from the second to the sixth years of age, beginning, according to Quain and Sharpey, at the *lowest* or fifth vertebra, and going *upwards*. Besides these, there are two *characteristic* points of ossification found in each of the three first sacral vertebræ, which are placed immediately above the three upper anterior sacral holes, exactly in the line of pressure from the ilia to the median line (*b*). These appear, from *above downwards*, at the same time as the posterior lateral centres just described. They unite first with the posterior lateral osseous points of their respective vertebræ, and with them join their respective central masses. Consequently, the three first sacral vertebræ have each *five* primary ossific centres, and the two last, each only *three*; the whole number of *primary* points of ossification in the sacrum being thus twenty-one.

At the age of sixteen years, the epiphysial or *complementary* ossific points begin to form, viz.: — On each articulating surface of the bodies of the sacral vertebræ is developed, as in the true vertebræ, a *horizontal plate* of bone, which, after coalescing with the bodies to which they respectively belong, finally (except the first and last) become soldered to each other from *below upwards*, commencing with the two last vertebræ, at from the sixteenth to the eighteenth years, and completing the formation of the sacral bone by the union of the two first vertebræ, at from the twenty-fifth to the thirtieth years. Between the eighteenth and the twentieth years begins the formation, by scattered granules, of four *lateral plates* of bone — one on each side, forming the iliac articular surfaces, opposite to the three first vertebræ — and one on each side, opposite the two last. These unite with the sacral bone about the same time that its upper vertebræ coalesce. The number of *complementary* points of ossification in the sacrum will thus be found to be *fourteen*, and the total number of sacral ossific centres thirty-five. M. Weber, however, assigns nine points of ossification to the first, seven to the second, and five to each of the three lower.

The *coccyx* is ossified by a single centre for each of its four pieces. Occasionally, in one of the upper are two ossific points. That of the highest piece first appears about the time of birth; that of the second bone is next evident, according to Beclard, at from five to ten years of age; the third, at from ten to fifteen years; and the fourth, at from fifteen to twenty. The two upper first unite together, then the two lower, the bone being consolidated by the union of the two resulting portions at various periods of life. In advanced life, and, more frequently, in the male subject, this bone is often found ankylosed to the sacrum. According to M. Weber, each coccygeal vertebra has two to four points of ossification.

Pelvic Articulations and Ligaments. — The *articulations* of the pelvis arrange themselves into; 1. those connecting the pelvis with the spinal column, or *lumbo-pelvic articulations*; 2. those of the pelvic bones with each other, or *proper pelvic articulations*; 3. those connecting them with the thigh bones, or *femoro-pelvic articulations*. The second class of articulations are those with which we have more immediately to do. The first class may be alluded to as necessary for elucidation of the subject. The last class come more particularly under the consideration of the hip joint.

The *ligaments* of the pelvis are of two kinds: 1. those which are closely connected with the several articulations, or *intimate ligaments*; and, 2. those which connect distant portions of its osseous structure, and are complementary to the articulations or *accessory ligaments*. The former will be best described with the articulations of which they form part.

Lumbo-pelvic articulations. — The sacrum, and through it the pelvis, is united to the last lumbar vertebra by exactly the same means as the vertebræ to each other, viz.:— First, by an *amphi-arthrodial* joint, composed of a thick *disc* of fibro-cartilage intervening between, and adherent to, their opposing articular surfaces; and strengthened by a continuation of the anterior and posterior common ligaments to the sacrum. Secondly, by two *arthrodial* joints invested with capsular ligaments, one for each of the articular processes. Thirdly, by the lowest members of the *ligamenta subflava* connecting the laminæ of the vertebræ with those of the sacrum, and by the lowest *inter-spinous* and *supra-spinous* ligaments connecting their spines. And, lastly, by an accessory ligament, which is a representative of the inter-transverse or oblique transverso-costal ligaments. This extends from the lower border of the last lumbar transverse process on each side, to the lateral masses of the base of the sacrum, its fibres expanding to the sacro-iliac symphysis and iliac crest. It is called the *sacro-vertebral* or *lumbo-sacral ligament*.

The fibro-cartilaginous *disc* is composed, like the other intervertebral plates, of an obliquely intersecting layer of fibres externally, and of a central, soft, pulpy portion, and differs only by gradually becoming much thicker anteriorly, like the body of the last lumbar vertebra itself. This allows of the curve of the spinal column at this part, which is the most salient point of the sacro-vertebral angle.

The *movements* of this joint are a limited antero-posterior motion with slight lateral flexure, somewhat less than that of the rest of the spinal column.

Proper or intra-pelvic articulations. — These consist of a joint uniting the sacrum and coccyx by a miniature *amphi-arthrosis*; of a joint on each side uniting the sacrum to the innominate bone posteriorly; and a single joint in front, uniting the innominate bones to each other. The three latter joints are of the kind usually denominated "*symphysis*," and considered by many as included also in the class "*amphi-arthrosis*."

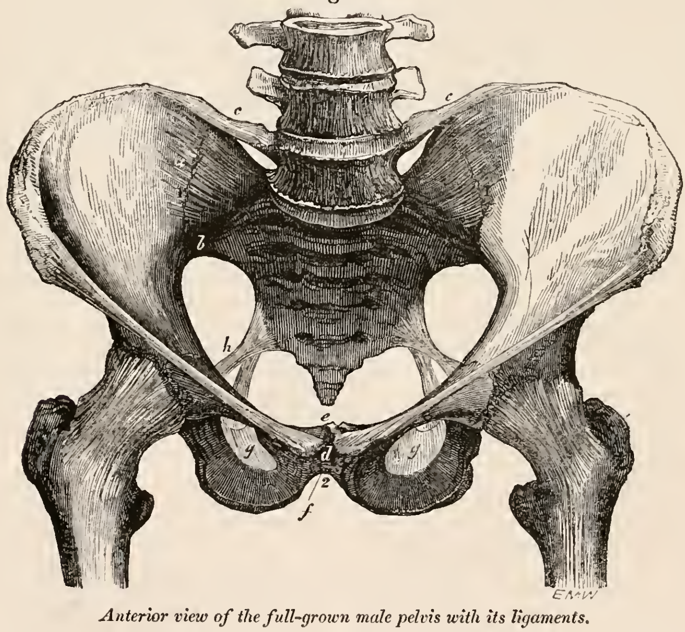
The sacro-iliac joints, however, most frequently presenting two *contiguous* surfaces and two separate plates of incrusting cartilage, ought rather, as Albinus remarked, to be considered as "*arthrodial*" forms of articulation, while the pubic symphysis occupies an intermediate or transitional position between the *fibro-cartilaginous* or *mixed*, and the *arthrodial* joints.

The *sacro-coccygeal joint* is composed of a fibro-cartilaginous *disc*, and an *anterior* and *posterior ligament*. The fibro-cartilaginous *disc* is a miniature of the intervertebral, intervening between and adherent to the opposed articular surfaces of these bones, being, however, less evidently pulpy in the centre. According to Cruveilhier, there is sometimes found a synovial membrane in the centre of this joint. The *anterior sacro-coccygeal ligament* consists of a thin layer of fibres passing from one bone to the other in front of the joint, and spreading over the whole coccygeal surface. The *posterior sacro-coccygeal ligament* is much stronger and more developed. It springs from the edges of the notched inferior opening of the sacral canal by a thick band of fibres, which includes also, as an investing capsular ligament, lined by a synovial membrane, the articular extremities of the sacral horns, and, gradually narrowing downwards, is attached to, and extends over, the whole posterior surface of the coccyx and its articular processes, covering in the inferior aperture of the sacral canal, and connecting the several pieces of the coccyx when they remain separate. In the latter case also are found *intra-coccygeal* articulations, small fibro-cartilaginous discs intervening between the several bones. This, according to Levret, is most constant between the first and second pieces of the coccyx, where it is sometimes met with in advanced age.

The *motions* of this joint, and those of the coccygeal bones, are simply antero-posterior flexure, and are sometimes, especially in females and young subjects, very extensive, forming, Cruveilhier says, a complete anterior projecting angle. This anatomist also mentions having seen many times *anterior* sacro-coccygean muscles; other anatomists also mention *posterior* sacro-coccygean muscles blended with the fibres of the ligament.

The *sacro-iliac joints* (*fig.* 80. 1.), one on

Fig. 80.



Anterior view of the full-grown male pelvis with its ligaments.

1, sacro-iliac symphyses; 2, pubic symphysis. *a*, superior sacro-iliac ligaments; *b*, anterior sacro iliac ligaments; *c*, ilio-lumbar ligaments; *d*, anterior pubic ligament; *e*, superior pubic ligament; *f*, subpubic or arcuate ligament; *g*, obturator membrane; *h*, sacro-sciatic ligaments; *i*, sacro-lumbar fibro-cartilage, forming the sacral promontory.

each side, are composed of an anterior or inferior portion, in which the opposing bones are covered with *cartilages* of an auricular or angular shape, and a posterior or superior portion where they are united by powerful *inter-osseous ligaments*, which fill up the retiring angle left by the cartilages. These are inclosed by *anterior*, *posterior*, and *superior* sacro-iliac *investing ligaments*.

The *cartilages* lining these articulations differ from those in the pubic symphysis in being almost totally wanting in the fibrous elements which are in the latter joint intermingled with them. Under the microscope a section of the sacro-iliac cartilages presents the ordinary appearance of cartilage incrusting the surfaces of arthrodial joints. They have been said by many writers to be completely incorporated together so as to form but one mass; but such is not the conclusion I have come to, except in a few cases, after many examinations carefully made in subjects recently deceased. The cartilages are very strongly adherent to, and follow exactly the shape of, the auricular articulating surfaces of the sacrum and ilium before described, their rounded projecting angles being the most depending part of the articulation. That on the sacrum is almost double the thickness of the iliac cartilage, which is somewhat less than one eighth of an inch thick. In the male, in a few instances, the two seem to project into each other by irregular prominences, and to be connected without the intervention of a regular synovial membrane. In these cases it has been remarked, that on the application of force, the cartilage separates from the ilium, leaving its auricular surface denuded. Much more frequently in the male, however, and always in the female and child, I have found, extending between them throughout, a completely smooth surface, apparently lined by a delicate *membrane*, and containing much thick synovia. The opposing cartilaginous surfaces are, in these cases, wavy or *ƒ*-shaped, when seen in a cross section, the sacral part being convex, and the iliac part concave in front, the reverse arrangement having place behind, the greatest depression being in the iliac surface, exactly at the angular junction of the two limbs of the auricular surfaces, at the most depending point of the articulation, and through which passes directly the line of pressure hereafter to be noticed (see *fig.* 89. *page* 144. *c, f*). At this point also, the breadth of the cartilaginous surface is the greatest, being generally about an inch. Towards the extremity of each limb the width gradually becomes less. The inferior or horizontal portion is longer than the other, generally being about two inches long, the superior or vertical portion being an inch and a half long.

Immediately posterior to, or rather above, this cartilage-covered surface, and filling up the digital depressions found there on each bone, are firmly implanted the *inter-osseous ligaments*, composing the remainder of the articulation. These consist of very strong and coarsely interlacing fibres passing almost directly from bone to bone, inclosing large meshes which are filled with a soft loose synovial looking fat, and containing many veins. Behind, these are continued into the deep posterior sacro-sciatic ligaments.

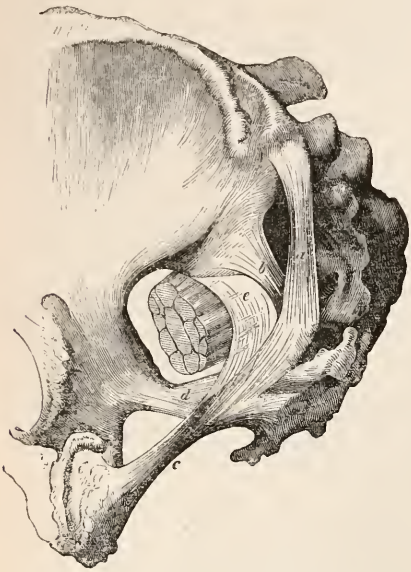
The *superior sacro-iliac ligament* (*fig.* 80. *a*) is a strong layer of fibres passing from the lateral masses of the sacral base to the posterior edge of the internal iliac fossa. It is continued in front to the *anterior sacro-iliac ligament* (*b*), similar in character to the last, but thinner and more feeble, passing from the first three bones of the sacrum to the superior border of the iliac notch. The former of these assist to prevent *downward* and *backward* displacement, and the latter *upward* and *backward* displacement; the position of the former being more anterior than superior, and the position of the latter more inferior than anterior in the proper position of the pelvis.

By far the most powerful of the ligaments of this articulation, and that which must be considered as the chief means of supporting the great downward pressure at this joint, are the *posterior sacro-iliac ligaments*. These are divided into *deep* and *superficial* layers of fibres.

The *deep* layer (*fig.* 89. *page* 144. *e*) passes from a well-marked prominence on the anterior surface of the iliac tuberosity, downwards and inwards, to the superior lateral part of the posterior surface of the sacrum, principally to the two upper pieces, external to the foramina; the fibres spreading out in interlacing bundles towards the broader surface of implantation on the sacrum, becoming longer as they become more superficial, and leaving meshes for the interposition of masses of loose fat, and the passage of numerous small veins. The erector spinæ muscles arise from the surface of this ligament, and cover it. To obtain a good view of these fibres, a transverse section along the brim of the true pelvis should be carried backward through the sacrum, as shown in the figures. This will show the manner in which the tuberosities of the ilium hang over the sacrum, suspended, as it were, between them by these ligaments. It will be more particularly explained when treating on the mechanics of the pelvis. The *superficial posterior sacro-iliac ligament* (*fig.* 81., next page, *a*) has been termed *oblique*, from the direction of its fibres; or *long*, from the extent of them. It is attached above to the posterior superior spine of the ilium, and passes downwards and obliquely a little inwards to be implanted into the fourth transverse tubercle of the sacrum external to the hole. To the sides of this ligament, which is almost subcutaneous, are attached the fascia lumborum and great gluteus muscle. This ligament is described by Cruveilhier to be attached to the third sacral vertebra. In all the cases I have seen, it is attached to the *fourth* transverse tubercle, which is the most prominent tubercular projection in the dried bone. Bichat erroneously calls it "*sacro-spinous*."

Attached to the same sacral tubercle, and passing *horizontally* outwards to be implanted into the posterior surface of the *inferior* posterior spine of the ilium, a point exactly corresponding to the termination of the horizontal limb of the sacro-iliac articular surface, is another well-marked ligament (*fig.* 81. *b*), which, being separated by a distinct cellular interval from the deep ligaments and distinguished by the more deeply seated position and horizontal direction of its fibres from the oblique ligament (*a*), and from the great sacro-sciatic ligament (*c*), I think merits the name of the *inferior* or *short superficial posterior sacro-iliac ligament*. This ligament has been hitherto apparently confounded with the great sacro-sciatic, which is attached to its lower border by a thin fibrous extension.

Fig. 81.



Posterior view of the ligaments of the pelvis.

a, oblique posterior sacro-iliac ligament; *b*, inferior posterior superficial sacro-iliac ligament; *c*, great sacro-sciatic ligament; *d*, lesser sacro-sciatic ligament; *e*, membranous expansion over the pyriformis muscle.

The ligaments which may be considered as *accessory* to this articulation are three in number — the *ilio-lumbar* ligament above, and the *greater* and *lesser sacro-sciatic* ligaments below.

The *ilio-lumbar* ligament (*fig.* 80. *c*) is a triangular fascicular ligament, thickest at the edges, and passing from the tip of the last lumbar transverse process, to which its apex is attached, horizontally outwards, and a little backwards to the posterior fifth of the inner lip of the crest of the ilium, along which its fibres spread as far forward as the inner projecting point of the posterior curve. To the outer side and behind this ligament is attached the quadratus lumborum muscle with the tendon of the transversalis abdominis, and to its front the psoas magnus muscle. Meckel describes this ligament as sometimes reaching as high as the transverse process of the fourth lumbar vertebra. He also describes a second ligament lower than the preceding, but arising from the iliac crest a little behind it. They are called by him, respectively, the *upper* and *lower anterior pelvic ligaments*, the latter corresponding to the sacro-vertebral ligament before described.

The *great sacro-sciatic ligament* (*ligamentum pelvis posticum magnum*, *fig.* 81. *c*) is attached behind, to the posterior inferior spine of the ilium by a membranous expansion (*e*); to the superficial posterior sacro-iliac ligaments with which its fibres are blended; to the posterior surface and borders of the two last pieces of the sacrum; and to the posterior sacro-coccygean ligament and borders of the two or three upper coccygeal bones. From this broad attachment its fibres pass downwards, forwards, and outwards to be implanted into the whole length of the raised inner border of the great tuberosity of the ischium. The fibres of this ligament are arranged in fasciculi, which cross each other in an X-like manner, so as to present, at the extremities, an expanded appearance, and in the centre a thick contracted rounded outline. The fibres which are placed superiorly in one extremity of insertion cross at the contracted part to become inferior at the other extremity, while those which are internal cross in the opposite direction to become external. Its superior border, consequently, is directed outwards and forwards, and its inferior border inwards, and both present a curvilinear outline. At its insertion into the sciatic tuberosity, the fibres of the lower border present a falciform margin having the concavity directed upwards along the inner edge of the tuberosity, where it is united to the fascia covering the obturator internus muscle. Its superficial or external fibres are continued over the tuberosity inferiorly into the tendons of the biceps flexor cruris, and semi-tendinosus muscles. Near the posterior extremity, this ligament is almost invariably perforated by a small hole, through which passes the coccygeal branch of the ischiadic artery. To the whole length of its external or posterior surface is attached the great gluteus muscle, which causes it when dissected to be very rough and flocculent. At the posterior half of its inner surface it is blended intimately with the lesser sacro-sciatic ligament, anterior to which it is smooth, and forms part of the boundary of the ischio-rectal fossa.

The *lesser* or *internal sacro-sciatic ligament* (*ligamentum pelvis posticum parvum*, *fig.* 81. *d*) lies internal to the last, in common with which it is attached posteriorly to the side of the two last pieces of the sacrum and of the two upper pieces of the coccyx. At its anterior extremity it is contracted into a pointed insertion into the spine of the ischium. The direction of this ligament is horizontally forwards and outwards, and its shape is triangular, so that its anterior contracted portion diverges from the great sacro-sciatic ligament, leaving a triangular opening between them through which pass the obturator muscle out of, and the pudic vessels and nerves into the pelvis This ligament, thus passing from the sacrum across to the ischium, converts the sacro-sciatic notch into a triangular or oval foramen through which pass the pyramidalis muscle, the gluteal, ischiadic and pudic vessels, and the superior gluteal and great and lesser sciatic and pudic nerves out of the pelvis. With its anterior or internal surface are blended the fibres of the ischio-coccygeus muscle, which exclude it from the ischio-rectal fossa, and render it rough when dissected.

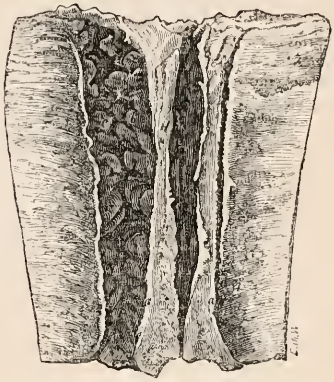
Sœmmering describes the lower part of the powerful lumbar fascia as a ligament connecting the ilia to each other posteriorly and to the lower spines of the sacrum. This fascia does, doubtless, act powerfully in clasping the ilia upon the sacrum between them. He calls it the *lateral sacro-iliac ligament*, or the *posterior lateral iliac ligament*.

The important part which these three accessory ligaments play in the mechanism of the pelvis will be hereafter shown.

The *movements* of the sacro-iliac joint are very limited indeed, its principal characteristic being compactness and strength, with just sufficient sliding motion downwards and backwards to break the shock of concussion passing from the lower extremities to the trunk. This is said by some to be increased in pregnancy and by parturition.

The *pubic symphysis* (*fig.* 80. 2) is an azygos joint uniting the innominate bones by their pubic portions in front. The osseous surfaces composing it are oval, with the long diameter directed downwards and backwards, and generally an inch and a half long, by three quarters broad. The planes of these surfaces not being directly opposed to each other, leave a larger interval of separation in front than behind. This interval is filled by a fibro-cartilaginous *disc*, which is correspondingly thicker in front, where the fibrous components are so numerous and strong as to constitute almost an interosseous ligament, and pass from one bone to the other in an oblique and concentric direction. Towards the central and posterior part this disc is generally mainly cartilaginous in structure, and is often, in females, separated in the middle by a chink forming two smooth, plane, oval contiguous *articular surfaces*, of various dimensions, sometimes irregularly laminar, at others with a delicate investing membrane. In parturient women these surfaces often extend over nearly the whole of the articulation, and are well marked in a figure given by Dr. Hunter, in the second volume of *Medical Observations and Inquiries*. In males, this separation is seldom present. The whole of the disc may, however, by maceration, generally be separated into two *plates* (*fig.* 82. *a*, *a*), of a denser and more cartilaginous structure than the rest, each strongly adherent to the bone by *mammilliform fibrous processes* (*b*), which pass into corresponding depressions in the osseous surfaces (*c*), and are connected to each other on opposite sides, by continuation of their fibres, arranged in oblique and concentric layers, which interlace obliquely with each other. (*d*) Dr. W. Hunter remarks, with Sandifort and Albinus, that the two cartilaginous plates (*a*,*a*), covering the opposed surfaces of the ossa pubis, are usually connected by a structure rather ligamentous than cartilaginous; and in a memoir on the pubic symphysis, gives an engraving of this arrangement. In several instances I have seen the fibrous processes which connect the plates with the bone very well marked, leaving on the bone, after maceration, deep conical pits. The above figure was taken from a macerated preparation of this joint. According to the observations of Tenon, these processes are directed into the bone downward and backward, as well as outward, and tend to prevent displacement of the cartilage in that direction. The *inter-laminar fibro-cartilaginous tissue* is very elastic and yielding, swelling out on the cut surface when lateral pressure is made on the bone, somewhat in the manner of the intervertebral discs. It often evinces a tendency to split in a lamellar direction after maceration. Around the circumference the concentric fibres become much more numerous and strong, and are continued into the peripheral ligaments. These are an *anterior*, *posterior*, a *superior*, and an *inferior* ligament.

Fig. 82.



Symphysis pubis after maceration.

a, cartilaginous plates of Dr. Hunter; *b*, mammillary processes on their osseous surface; *c*, corresponding osseous depressions to receive them; *d*, inter-laminar concentric fibro-cartilaginous tissue divided vertically in the centre.

The *anterior pubic ligament* (*fig.* 80. *d*) is a thick layer, passing between the anterior surfaces of the bones, strengthened by and blended with the oblique fibres of the aponeurosis of the external oblique muscle continued to the opposite pubic bone in front of the joint.

The *posterior pubic ligament* is the most feeble. It is composed of transverse fibres, somewhat scattered, and is remarkable in being raised by the posterior border of the pubic fibro-cartilage into a vertical ridge, in old persons often very evident to the touch. It gives attachment to the superior true ligaments of the bladder, and the anterior fibres of the levator ani muscle.

The *superior pubic ligament* (*e*) is formed by a thick, smooth layer of fibres often raised by a central ridge like the posterior, passing between the crests of the pubes, the superficial fibres extending over the greater part of the crests, and giving origin to the recti abdominales and pyramidales abdominal muscles, and linea alba.

The *inferior* or *sub-pubic ligament*, (*ligamentum arcuatum*, *f*) is the most powerful, passing from one descending ramus of the pubis to the other in an arched form. Its place of attachment to the pubis is often a well-marked surface, triangular, with the base upward, and half an inch in depth, corresponding in this respect to the outline of the section of this ligament. This ligament and the anterior are the most intimately connected with the fibro-cartilage of the joint. It unites below with the two layers of the deep perineal fascia or triangular ligament, between which it gives origin to the vertical compressores urethra, and forms the superior boundary of the pubic arch, the apex of which it rounds off and smoothens.

The *movements* of the pubic symphysis are confined to a slightly yielding sliding motion giving elasticity to the resistance of the pelvic ring.

The *obturator* or *thyroid membrane* (*g*) is a fascial aponeurosis rather than a ligament, which closes in the oval foramen of that name. It is composed of layers of fibres, intermingling in a circular direction, and generally congregated more in some places than others. These are attached to the rough narrow border of the descending branch of the ischium externally, but at the internal half of its circumference it is attached to the posterior *surface* of the ascending branch of the ischium and descending branch of the pubis, overlapping in this situation the borders of these bones posteriorly. Superiorly, it is interrupted by passing over from one edge of the sub-pubic notch to the other, so as to form the lower boundary of a foramen for the passage of the obturator nerves and vessels. Opposite the cotyloid notch its fibres are continued into the capsular ligament investing the hip joint. By its anterior surface, it gives attachment to the obturator external muscle, and, by its posterior surface, to the internal muscle of the same name. It is sometimes deficient in one or more places.

General appearance of the articulated Pelvis.—When the bones of the pelvis are articulated together, its whole appearance is that of a section of a cylinder or bent tube, having an *anterior*, *posterior*, and two *lateral*, and a *superior* and *inferior* aspects.

Its *anterior aspect* (*fig.* 80.) is bounded on each side by a line passing from the anterior superior iliac spine, along the anterior border of the cotyloid cavity to the ischiadic tuberosity on each side. It presents the pubic symphysis directed downwards and forwards in the median line, and the obturator foramina directed forwards, outwards, and downwards on each side. As first noticed by Cuvier, this oblique direction of the symphysis pubis is peculiar to the human species, that of animals being parallel with the axis of the body. In addition to these parts, already described, are two large notches formed by the approximation of the innominate bones. Of these the superior one, which may be called the *ventral notch*, is formed by the vertical and horizontal portions of the anterior border of the innominate bones on each side with the peculiarities before mentioned in its description. In the natural position of the pelvis this notch exposes to the view most of the internal surfaces of the pelvis to be described from the superior aspect. The inferior notch is formed by the oblique ascent towards the symphysis pubis of the branches of the ischium and pubis, forming what is termed the *sub-pubic arch*. Its apex is limited by the arched sub-pubic ligament, and there, in the male, it is generally about an inch wide, and at the base, between the ischiadic tuberosities, about three inches wide. The edges of this arch are in both sexes projected forwards, more or less, so as to present an inclined surface to the plane of the arch. This eversion as well as the measurements are, however, considerably greater in the female pelvis, hereafter to be considered.

The *lateral aspects* of the pelvis present the anterior half of the external surface of the ilia above; the cotyloid cavities directed outwards, forward and downwards, in the middle; and the descending branch and hinder part of the tuberosity of the ischia below, the latter being directed outwards and backwards.

The *posterior aspect* presents the posterior surface of the sacrum and coccyx in the centre, the most prominent point, in the erect position of the body, being the divided spine of the fourth sacral vertebra. On each side, next in succession, occur the overhanging and projecting tuberosities of the ilia, constituting two prominences next in importance, concealing the sacro-iliac articulations, and causing the lateral parts of the three upper sacral bones to appear as a deep groove on each side for the reception and origin of the powerful erector muscles of the back. Between these points also the last lumbar vertebra appears sunk between the two iliac crests, so that its upper surface is on a level with their most elevated central portion. Below the sacrum, the coccyx projects downwards and forwards in a salient median point, which separates and completes the inner boundary of the sciatic notches on each side, converted into foramina by the greater and lesser sacro-sciatic ligaments. The distance of the edges of the sacrum and coccyx from the spines and tuberosities of the ischia, and consequently the size of the openings, is less in the male than in the female; but the depth of the notches vertically is greater in the former. Above these are seen the posterior half of the external iliac surface, or external iliac fossa, surmounted by the rising crest.

The *superior aspect* (*fig.* 80.) reveals to view the whole of the *internal surface* of the pelvis, which presents two well contrasted portions, divided by a rounded edge or border, of which the superior is wide, expanded, and deficient in front, and is called the *large*, or *false pelvis;* and the inferior, narrower, more complete, and more compact, is called the *small*, or *true pelvis;* while the border which separates them is commonly expressed as the *brim*, or *superior outlet* of the true pelvis.

The *false pelvis* is formed laterally by the concave surface of the internal iliac fossæ directed upwards, forwards, and inwards; and posteriorly by the lateral masses of the base of the sacrum, directed upwards and forwards. In the middle is also seen, in the articulated pelvis, the anterior surface of the body of the last lumbar vertebra, filling up, with the pelvi-lumbar ligaments, the notch otherwise left between the ilia behind. The superior border of the false pelvis is formed by the ilio-lumbar ligaments (which exclude the iliac tuberosities), and the anterior three-fourths of the iliac crest, the most prominent point of which, in the proper position of the pelvis, is the centre of the posterior curve. It is terminated suddenly, in front, by the anterior superior iliac spine, where the ventral notch commences: by the deficiency of osseous structure at this part.

The *brim of the pelvis* is a heart-shaped opening, formed posteriorly by the body of the first sacral vertebra which overhangs the cavity of the true pelvis, so as to form a projection called the *promontory of the sacrum* (*i*), corresponding to the indentation in the emblematical heart-shape. On each side of this, the rounded arched anterior borders of the lateral masses of the sacral base continue the brim across the sacro-iliac joint, to the thick rounded ridge on the inner surface of the ilium, which is prolonged behind the ilio-pectineal eminence to the horizontal branch of the pubis where the brim becomes identified with the pectineal line. Finally, the brim is completed anteriorly by the shelving border of the body of the pubis, immediately behind the crest, and by the rounded superior part of the pubic symphysis. The part of the brim of the pelvis which is formed by the two portions of the innominate bone is sometimes called the *linea ilio-pectinea*, or, by some, the *linea innominata*. Sometimes the brim is called the *inlet* of the true pelvis.

The *cavity of the true pelvis* is formed laterally by the plane sloping inner surfaces of the lower part of the ilia, opposite the cotyloid cavities, and of the descending branches of the ischia, the latter being termed by obstetricians the *planes of the ischia*; in front, by the posterior surfaces of the branches and symphysis of the pubis, and by the ascending branches of the ilia; and behind, by the whole concave anterior surface of the sacrum and coccyx, the former being sometimes called the *hollow of the sacrum*. From the oblique position of the pelvis, the posterior wall, which is the deepest, also reaches the highest, and the lateral walls the lowest; the sub-pubic arch cutting out the anterior wall and leaving only the short symphysis pubis to represent it. The interval between the sacrum and ossa innominata behind, forming the sacro-sciatic notch, is completed and bounded by the sacro-sciatic ligaments, the inner surfaces of which are seen in this view. The inner surface of the coccyx is also seen to have an aspect directed upwards and forwards, and the spines of the ischia to project considerably inwards, so as to present two opposite points, the distance between which may sometimes be of great importance in parturition. This projection is much greater in the male than the female, and will be alluded to in the relative measurements of the pelvis. The cavity of the pelvis contracts uniformly downwards at the sides by reason of the inclination of the innominate bones; but, from the vertical curvature of the sacrum, the antero-posterior diameter is much greater in the middle than at the superior or inferior outlets, which are hence termed *straits*. The presence of the obturator foramina antero-laterally, and of the sacro-sciatic foramina postero-laterally, must also be remarked as constituting four openings, diagonally opposed to each other, capable, from the yielding nature of the structures filling them, of enlarging these diameters under sufficient pressure The great projection, forwards, of the coccyx and lower end of the sacrum may be considered as compensated for by the deficiency of the anterior wall in the sub-pubic arch directly opposite to them, gradually widening downwards as they advance. Both the forward direction of the coccyx, and the width of the pubic arch, are peculiar to the human species, and have reference to the erect posture.

The *inferior aspect* of the pelvis presents to view the *inferior strait*, or *outlet of the true pelvis;* which, on account of its more limited extent than the superior outlet, reveals nothing of the interior save the overhanging promontory of the sacrum. It is remarkable in presenting three bony *prominences*, viz., the two tuberosities of the ischia laterally, and the coccyx posteriorly, separated by three *notches*, placed opposite to each prominence respectively, viz., the sacro-sciatic, postero-laterally, and the sub-pubic notch anteriorly. The sacro-sciatic notches being closed by the great sacro-sciatic ligament, the completely formed opening thus assumes a lozenge shape, of which the lower part of the pubic symphysis and the tip of the coccyx form the extremities of the long diameter; the tuberosities of the ischia those of the short diameter; the oblique united rami of the ischia and pubes the antero-lateral, and the great sacro-sciatic ligaments the postero-lateral sides. Of these boundaries it is to be especially remarked, that the coccyx and those parts of the ligaments which are attached to it, are not *fixed* like all the previously described boundaries of the pelvis, but *movable*, on the sacro-coccygeal articulation, and consequently, the diameters of this outlet dependent upon them, viz., the antero-posterior and the oblique or diagonal, are increased or diminished by the movements of this joint backwards or forwards. The only fixed diameter of the inferior outlet of the pelvis is the transverse one between the ischial tuberosities. Of the prominent osseous points here seen, the lateral ischial tuberosities descend much lower than the symphysis pubis and coccyx, on account of the wavy outline and oblique direction of the innominate bones. It is upon these tuberosities only, consequently, that the trunk rests in the sitting posture, and not upon a tripod formed by them and the coccyx, as has been erroneously supposed by some older writers. The boundaries of the inferior outlet, from the same cause, do not, like those of the superior, lie all in one plane or level, but are bent, as it were, at the ischial tuberosities, into two planes; an anterior, terminated by, and nearly in a line with, the symphysis pubis, looking downwards and a little forwards; and a posterior, terminated by and including the coccyx, directed downwards and backwards, parallel with the superior pelvic plane, but varying with the extension of the coccyx downwards. The plane of this outlet, however, is usually considered to be marked by a straight line joining the lower border of the symphysis pubis and the tip of the coccyx; and its general direction to coincide with a line drawn perpendicular to this plane downwards and backwards.

Differences of the pelvis in the sexes. — Of all the bones in the human skeleton, those of the pelvis offer the most distinct characters between the male and female sex.

In the *female* (*fig.* 83.), the bones are lighter, shorter, and broader, less evidently marked by tuberosities and indentations resulting from the attachments of the tendinous structures, and have in a less degree the peculiarities, before described, of the articulations, as well as those resulting from their peculiar mechanism. The *iliac crest* is less arched, and presents less distinctly the *S*-like curve, the *iliac wings* are thinner and more expanded, and the *internal iliac fossæ* larger, mare shallow, and directed more anteriorly, and the *iliac ridge* extending between the cotyloid and sacro-iliac joints is less massy, less suddenly arched, and longer. The *ischia* do not converge so much towards the inferior outlet, and with the *tuberosities* are less massy, wider apart, and shorter, and the *spines* are less marked, and directed less inwards, and the *transverse diameter* of the *inferior strait* is greater. The *ascending branches* and the *descending branches of the pubes* are thinner, narrower, and more oblique, turn their inner borders more forwards, and at the same time afford a more rounded expansion to the *pubic arch*, at the expense of the *obturator foramina*, which are thereby rendered smaller and more triangular in the female. The *symphysis of the pubis* is not so deep, and the fibro-cartilage is wider, thicker, and more vertical in position; the united *angles* are more flattened posteriorly, and the *horizontal branch* is longer, thinner, and directed more transversely outwards, rendering the distance between the symphysis and the cotyloid cavity, and consequently the *projection of the hips* greater, and an increased *transverse diameter* of the *brim*.

The *sacrum* is wider and less arched transversely, and its *promontory* does not so much overhang the pelvic cavity, and thus the *superior outlet* has less of the heart shape, being in females more properly termed oval. This difference of shape is also contributed to by the less lateral obliquity of the superior branch of the pubes.

Whether the sacrum is less *arched transversely* in the female, I endeavoured to ascertain by observations taken from eighteen subjects, of which half were male and half female. A strip of lead $\frac{1}{8}$th of an inch thick was made to assume the form of the transverse curve of the sacrum, by being pressed across the anterior surface just below the promontory, and the breadth from one sacro-iliac joint to the other carefully marked off. From this, a line was drawn on paper, following the curvature retained by the lead, the extremities of which line were joined by a straight line, forming a chord to the sacral arc. The distance of the centre of this chord from the centre of the sacral curve was then measured. In the nine males, the height of the arch thus obtained varied from six to nine lines; in the nine females, five to nine lines,— the greatest number of the males being seven lines, and the greatest number of the females being six lines. In the single case of the female where the measurement was nine lines, the subject was old. When we consider, that in the great majority of instances the breadth of the sacrum *measured along the curve* was greater by $\frac{1}{4}$ to $\frac{1}{2}$ an inch in the female, these results will yield a still greater relative depth to the transverse sacral curve of the male.

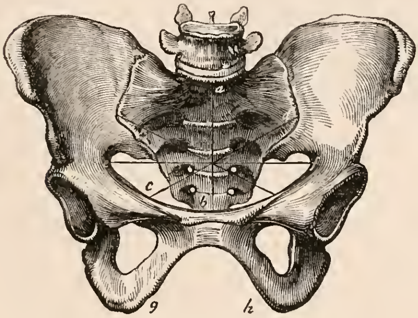
Besides this transverse arch, the *vertical curvature* of the sacrum is relatively much less in the female. This is more apparent in the direction of the three upper sacral pieces, which are generally little curved, and often almost plane in the female, while, in the male, the curve is most apparent in the centre and more uniformly distributed over the whole sacral surface. Upon this point, however, much difference of opinion prevails amongst anatomists; Meckel and Ward agreeing with the opinion here enunciated, while Cloquet and Cruveilhier maintain that the curvature of the sacrum in the female is *deeper* and more regular. The experiments of Mr. Ward, however, correspond more entirely with my own observations on this point. Mr. Ward observes, in addition, that the male sacrum often approaches the form of the female, but the female rarely to that of the male. In old women, however, I have often seen a great vertical curvature of the sacrum.

The *coccyx* is more moveable, more frequently in several jointed pieces, less projected forwards, and less frequently ankylosed to the sacrum in the female.

The *sacro-sciatic notches* in the female are wider and not so deep as in the male; the distance from the ischiadic spine and tuberosity to the sacrum and coccyx being greater, and the sacro-sciatic ligaments longer and more slender.

The peculiarities above mentioned give to the female pelvis a wider, shallower, more open, and less massy appearance than that of the male, and give rise to a still more important distinction derived from the *measurements* from one point to another, and from the relative *diameters* of the cavity and outlets of the pelvis. Another distinction will be presently found in the relative *angles* which the sacrum and whole pelvis form with the axis of the spinal column, and this again will influence the relative direction of the *axes* of the cavity and outlets.

Fig. 83.



Anterior view of the female pelvis, with lines of measurement.

a b, conjugate diameter of brim; *c d*, diagonal ditto; *e f*, transverse ditto; *g h*, transverse diameter of inferior outlet.

The measurements of the pelvis.—The most evident distinctions between the adult pelves of the sexes are derived from their comparative dimensions, and result from the important bearing they have upon the mechanism of parturition in the female. For this purpose, an average is taken from the measurements of many well-formed pelves, and one with the average results is adopted as the *standard pelvis*.

The measurements referring to the width of the pelvis are commonly spoken of as the *diameters* of the pelvis. They are taken at the brim, in the cavity, and at the inferior outlet, and are usually an *anterior-posterior* or *conjugate*, two *diagonal* or *oblique*, and a *transverse*.

At the *brim* of the pelvis, the antero-posterior or conjugate diameter is the distance between the upper part of the posterior surface of the symphysis pubis and the promontory of the sacrum (*a*, *b*, *fig*. 83.); the oblique, between the point of the brim nearest the pectineal eminence and the sacro-iliac joint of the opposite side (*c*, *d*); and the transverse diameter is the distance between the ilia at a point halfway between the sacro-iliac joint and pectineal eminence (*e*, *f*).

In the *cavity*, the antero-posterior diameter extends between the centre of the pubic symphysis, and the body of the third piece of the sacrum; while the oblique and transverse correspond to those of the upper outlet, on the same plane.

At the *inferior strait*, the antero-posterior extends from the lower extremity of the symphysis pubis to the tip of the coccyx; and the transverse, from the middle of the inner border of one ischiadic tuberosity to the other (*g*, *h*). An oblique diameter at the inferior outlet is not one commonly given by writers, although possessed of some importance in certain cases of deformity. In the table on the next page, there is the average of six measurements taken on the recent subject, before the shrinking of the ligaments, from the centre or junction of the ischio-pubic rami to the centre of the great sciatic ligament opposite. The antero-posterior diameter of this strait is capable of much increase by the mobility of the coccyx, which will also affect, in some measure, the oblique diameters, in an *opposite* degree, from the stretching of the great sciatic ligaments, a point which I think has scarcely been sufficiently noticed by accoucheurs.

Besides these, the distances between many other points may be of great importance to the accoucheur. Such are those pointed out by Naegele, to be presently noticed; the distances between the spines of the ischia, so much greater in the female; and another, which I have not hitherto seen definitively given, viz. the distance between the *lower edge* of the *symphysis pubis* and the *sacral promontory*, a measurement of considerable importance in the use of pelvimeters, to ascertain the conjugate diameter of the brim. This may be called the *lower* or *inclined conjugate diameter*, and it will be found to be, in most instances, half an inch more than the direct or superior conjugate diameter, being, in fact, the longest side of a triangle, having the conjugate diameter, and the breadth of the pubic symphysis for the other sides. The measurement of the *circumference* of the brim of the pelvis, and the proportion contributed to it by the sacrum, ilia and pubes respectively, announce a manifest difference between the pelves of the two sexes.

In glancing over the appended table, it will be seen that the male pelvis exceeds the female in most of its vertical dimensions, while the female pelvis is larger in the horizontal diameters. The depth of the true pelvis, however, measured at the sacro-coccygeal column, is greater in the female, on account of the greater size of the sacrum in that sex, and also because of the less total *vertical* curvature. The depth from the pectineal eminence to the lowest point of the ischiadic tuberosities laterally, and at the pubic symphysis anteriorly, show, on the contrary, a great superiority in the male; as also does the total depth of the whole pelvis, from the highest point of the ilium to the most depending part of the ischium, while the width between the iliac spines and crests are much greater in the female. The horizontal diameters of the pelvis may be said to depend upon the *ilio-pubic element*, while the depth or vertical measurement depends solely on the *ilio-ischion element*, so that, in the female, the former may be considered to prevail, and in the male, the latter element. This is remarkable, as constituting the different pelvic properties of certain classes of animals.

It will also be observed that the transverse diameter of the brim is the greatest in the dry bones, but this is so diminished by the presence of the iliac and psoas muscles and fascia, that, in the living female subject, the oblique is generally the best adapted to receive the long diameter of the fœtal skull. The soft structures diminish the antero-posterior diameters of the *brim* by about a quarter of an inch, and the transverse, by half an inch; the diameters of the *cavity* being lessened about a quarter of an inch; a fact which it is necessary to bear in mind in estimating the width in the living subject. The measurements in the third double column were taken from fourteen male and eighteen female subjects in the dissecting room of King's College, London, and are compared in the first column with the contrasted measurements of the male and female pelvis given by Meckel, and quoted by most English writers on the subject; and in the second column with those given by John James Watt, in his work on the pelvis.

Diameters.	Meckel.		Watt.			
	Male.	Female.	Male.	Female.	Male.	Female.
	in. lines.	in. lines.	in. lines.	in. lines.	in. lines.	in. lines.
Of the brim—Transverse -	4 6	5 0	4 6	5 6	4 7	5 2
Oblique - - -	4 5	4 5	4 2	5 0	4 7	5 0
Antero-posterior - -	4 0	4 4[a]	4 0	4 9[a]	4 0	4 5[a]
Of the cavity—Transverse -	4 0	4 8				
Oblique - - -	5 0	5 4				
Antero-posterior - -	5 0	4 8	- -	- -	4 8	4 8
Of the inferior strait —Transverse (inter-sciatic) - -	3 0	4 5[b]	3 2	4 0[b]	3 5	4 4[b]
Oblique - -	- -	- -	- -	- -	3 2	4 0
Antero-posterior -	3 3	4 4	3 0	4 6	3 5	4 0[c]
Measurements.						
Between the anterior superior iliac spines - - - - -	7 8	8 6[d]	9 0	11 0[d]	8 8	10 0[d]
Between the centres of iliac crests	8 3	9 4[e]				
Depth of true pelvis — Between the upper and lower border of symphysis pubis - - -			1 10	1 6	2 0	1 7
Between the ilio-pectineal eminence and ischial tuberosity - - - - -			4 10	3 6	4 5	3 8
Between the sacral promontory and tip of coccyx			4 10	5 0	4 6	5 in. to 6 in.
Depth of whole pelvis — Between the iliac crest and ischial tuberosity -					8 7	7 5[f]
Between the anterior superior iliac spine and ischial tuberosity -					6 5	6 0
,, posterior superior iliac spine and ischial tuberosity -					6 0	5 5
Between the lower border of pubic symphysis and sacral promontory -					- -	4 7
,, spines of ischia - - - - - - -					3 5	4 3
,, sacro-iliac joints (greatest breadth of sacrum) - -					4 3	4 8[g]

[a] 4 inches (Burns, Ramsbotham, Lee, Cloquet, Velpeau, and Baudelocque). 4½ inches (Monro and Boivin). 4·3 inches (Rigby).
[b] 4 inches (Burns, Lee, and Cloquet). 4½ inches (Monro and Murphy).
[c] Increased to 5 inches or more by the mobility of the coccyx.
[d] 10 inches (Burns). 9·6 inches (Cloquet).
[e] 10 inches (Cloquet). 11 inches (Burns).
[f] 7 inches (Cloquet).
[g] 4 to 4½ inches (Cloquet).

The *circumferential measurement* of the *brim* in well-formed *males* gave in my own measurements 2 inches to each of the ilia, 3 inches to each of the pubes, and 4½ to the sacrum, which, allowing ¼ inch to each of the sacro-iliac cartilages and ¼ inch to the pubic, gives a total circumference of 15¾ inches. In the well-made *female* the ilia were found to be each 2½, the pubes each 3¼, and the sacrum 5 inches, giving, with the same allowance for the sacro-iliac cartilages and ½ inch for the pubic, a total of 17½ inches. Thus the superior size of the brim in the female seems to depend more upon the ilia than upon the pubes, although the *direct* distance between the ilio-pectineal eminence and the sacro-iliac joint differs little in the sexes, because of the greater curve made by the female ilia. The circumferential extent of the borders, at the plane of the *inferior outlet* in a female pelvis of average diameters, and dried with the sacro-sciatic ligaments attached, was 14 inches. In the fresh state it generally amounts to 15, as the ligaments shrink by drying, and would be extended to 16 inches, or more, by the extension of the coccyx and the elasticity of the ligamentous portions.*

* The circumferential measurement appears to be one not generally estimated as much as its utility in detecting variations of size depending upon *shape* would seem to call for, in the female pelvis. A reference to the subjoined table of *variations* of *dia-*

Burns gives also, in the female pelvis, the following distances:—

1. Between the symphysis pubis and inferior iliac spine, nearly - - 4 in.
2. „ sacro-iliac joint and the pubic crest of same side - - $4\frac{1}{2}$ „
3. „ sacral promontory and the obturator notch - - $3\frac{1}{2}$ „
4. „ sacral promontory and the acetabula $3\frac{1}{4}$ „
5. „ acetabula anteriorly - $4\frac{1}{4}$ „
6. „ posterior ridge of ilium and the superior and inferior anterior spines - 5 „
7. „ centre of iliac crest and the brim of the pelvis, direct - $3\frac{1}{2}$ „

One of these measurements was repeated by Velpeau, Stoltz, and Naegele, viz. from the sacral promontory to the centre of the cotyloid cavity, or sacro-cotyloid. Naegele in 54 and Stoltz in 40 female pelves, found the mean distance to be 3 pouces, 3 to 4 lignes (*pied du Roi*).

Dr. Murphy, considering that the true salient point or promontory lies on a level above the real pelvic brim, at the sacro-lumbar fibro-cartilage, gives also three more measurements made in the "inclined plane of the promontory," one *antero-posterior*, between the fibro-cartilage and the upper border of the symphysis, which he places at 4 inches, and two *lateral*, from the same point to the pectineal eminences, which are on an average about $3\frac{1}{2}$ inches, but which are seldom equal, because of the great tendency to deviation of this promontory from the median line. The latter seem to coincide almost with those given by Dr. Burns between nearly the same points, and the former with the conjugate diameter of the brim.

External measurements of the female pelvis, made on the living subject, have also been given, though from few data, as follows:—

1. External antero-posterior diameter, 7 to 8 inches.

2. External transverse, between iliac crests, 13 to 16 inches.

3. From great trochanter to the opposite sacro-iliac joint, 10 to 12 inches.

4. Depth of pelvis from top of sacrum to coccyx, 4 to 5 inches.

From the first of these, according to Baudelocque and Velpeau, 3 inches must be deducted for the thickness of the parietes, and from the second 4 inches. Boivin and Lachapelle doubted the utility of these measurements generally, because of the great variability in the thickness of the pelvic walls; and Dr. Davis has more recently found the thickness of the base of the sacrum to vary from 2 to 3 inches in 17 dead subjects.

The measurements of Naegele and Otto, with a view to determine the presence of obliquely deformed pelves, are of great importance in the practice of midwifery, and may be best given in this place. Out of forty-two female pelves of medium size, the best formed they could obtain, these observers found the following measurements:—

	Measurement. in.	lines.	Greatest Difference. lines.
1. From the sciatic tuberosity of one side to the posterior superior iliac spine of the other side - -	6	6	3
2 From the anterior superior iliac spine of one side to the posterior superior of the other side - -	7	3	3
3. From the spine of the last lumbar vertebra to the anterior superior iliac spine on both sides - -	6	8	4 to 5
4. From the great trochanter of one side to the posterior superior iliac spine of the other - - -	8	5	
5. From the middle of the inferior border of the symphysis pubis to the posterior superior iliac spine on both sides - -	6	4	2

Danyan, pursuing Naegele's system, found the great rarity of perfectly regular female pelves. Out of eighty female pelves he found fifty-nine differ, in the first measurement, from 1 to 6 lines. In the second measurement he found a difference, in fifty-eight pelves, of 1 to 11 lines; in the third, fifty-one differed from 1 to 7 lines; in the fourth, sixty-two from 1 to 9 lines; and in the fifth measurement, forty-eight pelves had a difference of from 1 to 9 lines. The table on the next page shows the great variety in the diameters of female pelves which may be considered as normal *pelves*. In males Dupuytren found the distance between the tuberosities of the ischia, in twenty-three subjects, to vary from 2 to $3\frac{1}{2}$ inches; and Velpeau, in forty subjects, to vary from $1\frac{3}{4}$ to 4 inches. In fourteen subjects I have found the least distance to be 3 inches, and the greatest 4 inches in the male, and measuring from the exact centres of the inner margin of the tuberosities. These observations on the male are of some importance with a view to the operation of lithotomy, when the stone is of great size.

Inclination of the Pelvis.—By making, in a well-formed subject, a direct vertical section of the spinal column, and drawing a line through the centres of the *bodies* of the axis and last lumbar vertebra, and by comparing with the transverse plane of such a

meter, will show how frequently the diameters are compensatory to each other; as this compensation may occur in *diameters not usually measured*, the circumferential extent seems in many cases to be required. Dr. Churchill gives the circumference of the brim as varying from 13 to $14\frac{1}{2}$ inches in the female, much less than I have generally found it on the fresh subject after the soft parts were removed.

line those of the superior and inferior outlets of the pelvis, the general inclination of the pelvis to the vertebral column is obtained. The line so drawn will generally be found to

VARIATIONS in the Diameters of healthy Female Pelves.

	Dr. Murphy (in 18 Cases).		Taken by the writer in the King's College dissecting rooms (in 18 Cases).	
	Extremes.	Most frequent.	Extremes.	Most frequent.
	inches.	inches.	inches.	inches.
Inclined plane of promontory—				
Antero-posterior - -	*$3\frac{1}{2}$ or $3\frac{3}{4}$ to $5\frac{1}{2}$	$4\frac{1}{4}$ to $4\frac{7}{8}$		
To left pectineal eminence-	*3 or $3\frac{1}{4}$ to $4\frac{7}{8}$	$3\frac{1}{2}$ to $3\frac{7}{8}$		
To right pectineal eminence	*$2\frac{7}{8}$ or $3\frac{1}{8}$ to $5\frac{1}{8}$	$3\frac{3}{4}$		
Brim—Antero-posterior -	*$3\frac{6}{8}$ or $3\frac{7}{8}$ to $5\frac{1}{4}$	4	$3\frac{3}{10}$ to $4\frac{3}{4}$	$4\frac{1}{2}$
Transverse - -	†$3\frac{3}{8}$ or $4\frac{1}{2}$ to $5\frac{5}{8}$	$5\frac{1}{2}$	5 to $5\frac{3}{4}$	5
Oblique { Left - -	*$4\frac{1}{4}$ or $4\frac{3}{4}$ to $5\frac{1}{8}$	$4\frac{7}{8}$ }	$4\frac{3}{4}$ to $5\frac{1}{2}$	5 and $5\frac{1}{4}$
Oblique { Right - -	*$4\frac{5}{8}$ or $4\frac{3}{4}$ to $5\frac{1}{4}$	5 and $5\frac{1}{8}$ }		
Between promontory and lower edge of symphysis pubis -	- -	- -	$3\frac{7}{10}$ to $5\frac{1}{4}$	$4\frac{3}{4}$ and 5
Cavity—Antero-posterior -	*$4\frac{1}{8}$ or $4\frac{1}{2}$ to $5\frac{7}{8}$	5	$4\frac{1}{2}$ to $5\frac{3}{4}$	$4\frac{3}{4}$ and $5\frac{1}{4}$
Transverse - -	*$3\frac{5}{8}$ or $4\frac{1}{4}$ to $5\frac{1}{8}$	5	- -	- -
Between ischiadic spines -	- -	- -	$3\frac{1}{4}$ to $4\frac{1}{2}$	$4\frac{1}{4}$
Outlet—Antero-posterior -	‡$3\frac{3}{8}$ to §$4\frac{7}{8}$	4 to $4\frac{1}{2}$	$3\frac{1}{2}$ to $4\frac{1}{4}$	4
Transverse - -	§$3\frac{1}{4}$ to ‡5	$4\frac{3}{8}$ to $4\frac{3}{4}$	$3\frac{3}{4}$ to $4\frac{3}{4}$	$4\frac{1}{2}$
Oblique (6 cases only) -	- -	- -	$3\frac{1}{2}$ to $4\frac{1}{4}$	4
Angle of pubic arch - -	45° to 100°	70° to 90°		

* Like male pelvis, diameters small.
† Smallest pelvis, transverse diameter of cavity $4\frac{3}{4}$, of outlet $4\frac{5}{8}$.
‡ Belong to the same pelves respectively (compensating diameters).

pass also through the bodies of the first dorsal and second lumbar vertebræ across their centres. The curved line of the vertebræ, in most well-formed subjects, cuts the straight line at these two points, in passing from the cervical to the dorsal, and from the latter to the lumbar curve.

The plane of the pelvic brim has been termed by Naegele and the brothers G. and E. Weber the *superior plane* of the pelvis, and that of the inferior outlet the *inferior plane*. These observers measured the angle formed by these planes with the ground-level in the standing position, *i. e.* with the horizon, or with a plane drawn horizontally, at right angles, to the above-mentioned transverse vertical plane, which, in the erect posture, was found to be perpendicular to the base of support. The angle which the superior plane of the pelvis forms with the transverse vertical plane or with the horizon is termed by them the *angle of inclination* of the pelvis, or the *pelvi-vertebral angle* (*fig.* 84. *page* 134.), (*a e*, *e c*).

It is remarkable that, in man only, are the boundaries of the superior outlet in one plane, *i. e. in man only is the direction of the superior pubic ramus in the same plane with that of the cotylo-sacral rib of the ilium.* In all other animals, as far as my own observations go, the pubis is bent backward or forward, so as to make an angle with the ilium, and the *pelvi-vertebral* angle is thus resolved into two angles, a *vertebro-iliac* and an *ilio-pubic*.

The angle of the *superior plane* was found by the Webers on the dead body, by fixing the connected spinal column and pelvis of a recent well-made subject, in plaster of Paris, to preserve the natural position, then making through the whole a direct vertical section, and afterwards measuring off the angles.

On making a transverse vertical section through the centres of the heads of the femurs and cotyloid cavities, they also found that, when the body is in the erect position and the pelvis at the proper angle, the cotyloid notch and depression, and the fibres of the ligamentum teres, have an almost *directly vertical direction*, and fall exactly in the transverse vertical plane of the vertebræ (*see fig.* 87. *page* 140., in which the line *a a'* lies in the plane of the transverse vertical section). It will be further seen, by inspecting the figure, that this plane, being continued downwards, crosses the obturator foramina, and falls very nearly in the line of suture of the ischio-pubic rami. And this will be found to be the case, with a plumb line dropped from the sacral promontory, which is cut by the above plane in the erect position of the pelvis. A detached pelvis may be placed in the erect living position, consequently, by keeping the posterior part of the notch the most depending point of the cotyloid brim, and its inclinations will then accord with those taken in connection with the spine.

In the consideration of these pelvic angles it must be borne in mind that the direction of the curve of the three last lumbar vertebræ, below the point where the great dorsal concavity terminates, is such that, if prolonged upwards, the axial line would pass out at the junction of the manubrium with the body of the sternum. This makes the *pelvi-lumbar* angle much *less* in man than the whole pelvi-vertebral; a circumstance to be borne in mind in comparing them with those of animals. In fact, the transvertical section just mentioned passes through the body of the third lumbar vertebra considerably posterior to its centre in most cases (*see a, b, fig.* 84. *page* 134.).

By an inverse method, proceeding on Roederer's plan from the horizontal plane (*fig.* 84. *g*, *d*), Naegele determined, with great care, the angle of the *inferior plane* of the pelvis in the living *female*. In 500 well-formed living females placed in the erect position, he measured the respective distances from the ground, of the tip of the coccyx, and of the lower border of the pubic symphysis. He found that in 454 the extremity of the coccyx was higher than the symphysis pubis, the greatest difference being 22 lines. In twenty-six only was it lower, the greatest difference here being 9 lines, and in twenty they were equal in height from the ground. In eleven pelves where he had the opportunity of verifying his observations after death, he found and figured one perfect pelvis, in which the tip of the coccyx was 8 lines higher than the lower border of the symphysis, which corresponded very nearly with the mean elevation of the coccyx above the symphysis, viz. 7·1 lines, drawn from the observations above detailed. From this he deduced the inferior angle of inclination of the pelvis (*f g d*) to be 10° to 11° with the horizon (*g*, *d*).

In a similar manner, in fifteen living *males* the brothers Weber ascertained the range of the altitudes of the coccyx and pubis to be from 10 millimetres, the extreme difference when the coccyx was lower, to 33·3 millimetres when the coccyx was higher than the lower border of the symphysis pubis, the mean height of the coccyx above the pubis being thus 23·1 millimetres. Then, by measuring the distance between the plumb lines dropped from each of these points, the coccyx and pubis, they ascertained the mean distance to be 75·8 millimetres. From these measurements they obtained the angle of the inferior pelvic plane with the horizon 16°·51. By measuring, in two dead subjects, the depth of the symphysis pubis, and the direct vertical distance from the tip of the coccyx to the sacral promontory, they deduced the angle of the superior pelvic plane. The superior angle, however, cannot with any certainty be calculated from the inferior in the living subject, on account of the uncertain length and curve of the sacro-coccygeal column.

In a well-formed or *standard* pelvis the two lines of the superior and inferior planes, when prolonged anteriorly, cut each other about 1½ inch anterior to and below the pelvis (at *c*), containing an angle of about 50° (*e c f*); but this will vary with the length of the sacro-coccygeal column.

According to Naegele the point at which the superior plane emerges posteriorly is also very variable. Most frequently it is the spinous process of the second lumbar vertebra, often that of the first, and sometimes between the second and third. Generally the upper border of the symphysis pubis was 3 inches, 9 to 10 lines lower than the sacral promontory, and on a level with the union of the second and third coccygeal bones. The sacro-vertebral projection I have generally found to be about the level of the anterior superior iliac spine in the male, and a little below this point in the female, in a straight position of the body.

The following table shows the pelvic angles of inclination in the sexes, and their difference in this respect, and is drawn from the above-mentioned experiments of the Webers on male, and of Naegele on female subjects.

	Male (Weber).	Female (Naegele).
Angle of Inclination of superior plane, or pelvic brim.		
With transverse vertical plane	155°	150° to 151°
With horizon	65°	59° to 60°
Of inferior plane, or outlet.		
With transverse vertical plane	106° 51′	101° to 102°
With horizon	16° 51′	10° to 11°*

By the inspection of the above table the greater inclination of the pelvis to the spine in the male will become evident, constituting another distinguishing characteristic of the sexes.

The older observers estimated the pelvic angles too low, as in the incorrect drawings of Albinus, Levret, and Cloquet, where the superior angle is given as 35° with the horizon, and, by Osiander, at 30°. Carus gives the superior at 55°, and the inferior at 11° with the horizon.

Angles of the anterior and posterior pelvic walls with the transverse vertical plane.—The pelvic inclination, in the opinion of Cruveilhier, depends upon the angle which the sacrum forms with the spinal column, giving more or less of obliquity to the innominate bones on each side. This angle (*fig.* 84. next page, *a e i*, and *fig.* 112. 1. *f a g*, *page* 173), which may be called the *sacro-vertebral angle*, I have, in as many opportunities as have occurred to me, endeavoured to ascertain and establish, with a view of comparing it with the pelvi-vertebral angle in the two sexes. To do this I made a vertical section of the pelvis (with as many vertebræ as possible attached to it), from behind forward in the median line, which showed clearly the angle made by the sacrum. Then, by intersecting the line of the transverse vertical plane of the spinal column drawn as before mentioned, by a line drawn in the mean direction of the three first sacral vertebræ through the centre of their bodies, angles closely approximative to the sacro-vertebral angle in the living subject were obtained, showing the following results:—

* Weber, however, found the angle of the inferior plane with the horizon to be but little less marked than that of the male; making it 4°·5 more than the angle of Naegele here given. Naegele remarks that the inferior angle is much more variable than the superior in ordinary cases.

In twenty-five males,

Nine were from 110° to 112°, five from 115° to 117°, nine from 120° to 125°, and two only 130°.

In twenty-five females,

Nine were from 120° to 125°, eight from 128° to 130°, five from 133° to 140°, two were 145°, and one, an aged subject, 118° only.

Fig. 84.

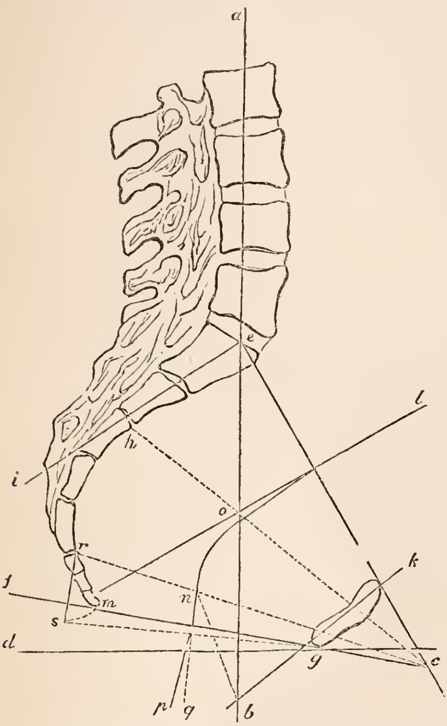


Diagram (slightly altered from Naegele) of a well-formed female pelvis, showing the angles of inclination and axes.

From these we may deduce 117° as the average sacro-vertebral angle in the *male*, and 130° as the same angle in the *female*. This remarkable average difference of 13° shows the much greater suddenness of the alteration of direction in the spinal column at its sacral extremity in the male subject, and is much greater than the difference of 5° to 6° in the pelvic inclination of the sexes compared in the tables of Weber and Naegele. But, in order more clearly to ascertain if the pelvic inclination invariably depended upon the variations of the sacro-vertebral angle, I compared the sacro-vertebral and pelvi-vertebral angles in nine male and nine female subjects. In the former, I found the *difference* between these angles to vary from 5° to 35°, and, in the latter, to vary from 5° to 25°. In one instance only, in a male, the sacro-vertebral was as large as the pelvi-vertebral angle. From these observations, which were very carefully taken, it would seem that *the total pelvic inclination does not exactly depend upon the sacro-vertebral angle;* and that, in *males*, where the average pelvic obliquity is *a little* greater, the average sacro-vertebral angle is *much* and *disproportionately* less. These results contradict, also, the assumption somewhat indefinitely stated by Blumenbach and others, on the authority of Bonaccioli, of Ferrara, that the sacrum inclines more backward, and that the sacro-vertebral angle is more prominent in the female than in the male.

If the long diameter of the pubic symphysis be continued in its direction downwards and backwards, it will, in a well-formed female pelvis, cut the transverse vertical plane of the spine, also prolonged, at an angle of 50° to 55° (*fig.* 84. *a b k*), which will be found to be about the complementary or opposite angle to the sacro-vertebral angle in the female. This shows the general parallelism of the anterior or pubic wall of the pelvis, with the upper part of the posterior or sacral wall, although, on account of the rapid thinning of the latter as it descends, its pelvic surface seems to diverge from the pubis. Naegele found the anterior pelvic wall to be often at right angles to the plane of the inlet, but the posterior generally somewhat more than a right angle. The great obliquity of the symphysis pubis to the transverse vertical plane of the vertebræ is one of the great characteristics of the human pelvis, as will be seen hereafter in the consideration of the comparative anatomy of the pelvis. The angle formed by the symphysis pubis with the horizon is given by Cuvier from 75° to 95°. This is much too large; from 35° to 40° is the true angle of the symphysis with the horizon in the human subject.

Ilio-ischial angle. — While the pubis in the human subject is continued in the same right line with the mean direction of the ilium, which coincides with the *cotylo-sacral rib* of that bone, the ischium is inclined *backwards*, forming an angle of 110° to 115° with the same rib of bone (see *fig.* 112. 1. *a c d*, *page* 73.), so that, while the pubes are directed *transversely* with regard to the pelvic cavity, the ischia are directed *vertically* along, and forming the sides of the cavity. This arrangement will also be found to be an important characteristic of the human pelvis, when compared with those of the inferior mammalia, in which the reverse of this arrangement will be found to prevail, viz., the continuation of the ischia in the line of the ilia, and the formation of an *ilio-pubic* angle.

Angle of ischio-pubic arch. — The angle at which the ischio-pubic rami tend toward each other, has been placed by Watt at 60° to 80° in the male, and 90° in the female; and by Sœmmerring at 75° for the male, and 95° for the female (*see figs.* 83, 80.).

Axes of the Pelvis. — The term axis is applied anatomically to the *line of direction* of any surface or plane, and, as it implies a right line, drawn at right angles to that surface or plane, it can only be applied with propriety to the outlets of the pelvis. As applied by some authors to the line which indicates the central point in any given plane of the pelvic cavity, it then becomes really a *curved* line, made up of an infinite number of perpendiculars drawn from any number of planes radiating from a centre placed anterior to the symphysis pubis. Since it is with regard to the mechanism of parturition principally that the axes of the pelvis are of importance, the angles formed by them, with the vertebral plane (transverse vertical), are stated in reference to the standard *female* pelvis more particularly. In the male subject, these angles will be somewhat greater, from the greater inclination of the pelvis in that sex.

The *axis of the brim* is a line drawn from the centre of the superior plane, and at right angles to it (*fig.* 84. *l*, *m*). This line cuts the prolonged vertebral plane exactly half-way between the symphysis pubis and the upper part of the third sacral vertebra, and forms with it an angle of about 60° (*a o l*). It may be taken also as the most nearly approximative axis of the pelvic *cavity* above that point. When prolonged at each end, it passes out at the umbilicus, and impinges upon one of the two last coccygeal bones, in a well-formed female. It is evident, however, that from the, great variety of the sacro-coccygeal curves, that the point where this line meets the coccyx will be variable. Hence, the observation of Watt, that a line joining the tip of the coccyx and the centre of the superior plane cuts the latter at an angle of 75°, is too definitive. M. Naegele, however, found that in a large number of female pelves, this line did meet the coccyx at some point or other.

The *axis of the inferior outlet* (*n*, *p*) is drawn at right angles to the centre of the inferior plane, and falls midway between the sciatic tuberosities. From the mobility of the coccyx, it will vary with the motion of that bone from its ordinary position to a position of extreme extension. In the ordinary position of the coccyx, this axis forms, with the vertebral plane, an angle of about 10°, and meets it near the centre of the upper surface of the body of the first sacral vertebra, impinging there upon the sacral promontory. When the coccyx is in a position of extreme extension, however, its tip describes the curve *m*, *s*, this axis is thrown more forward (*n*, *q*), and forms a less angle with the vertebral plane; while the plane of the inferior outlet itself is depressed (*g*, *s*), and its angle with the horizon (*s g d*) diminished.

The curved line (*l*, *o*, *n*, *p*), which indicates the *continued centres* of the planes of the pelvic cavity, may be divided into three portions indicated in the figure by the two dotted planes (*c*, *h* and *c*, *r*). The part from the plane of the outlet to the upper dotted plane (*c*, *h*), impinging upon the third sacral vertebra, may be considered to coincide, for all practical purposes, with the line of axis of the brim (*l*, *m*). The inferior dotted plane (*c*, *r*), drawn, like the former, from the point of junction of the planes of the brim and inferior outlet, to the tip of the last sacral vertebra, includes, with the upper dotted plane just mentioned, a *parabolic curve* (*o*, *n*), which does not quite coincide with the arc of a circle drawn from the ante-pubic centre (*c*). These two portions of the axes of the cavity are *fixed*, from the immobility of the pelvic walls which include them. But, below the inferior dotted plane to that of the outlet, the axis is directed more *forwards* (*n*, *q*), as the coccyx moves *backward* in the curve (*m*, *s*), a deviation which facilitates the exit of the fœtus in parturition. This forward direction of the axis at this part is increased also by the rounding off of the symphysis pubis at its inferior border. Each of the three portions passes midway between the corresponding and opposing surfaces of the symphysis pubis and sacro-coccygeal wall, the general vertical outline of which it nearly resembles, and between the lateral ilio-ischial columns. The latter, being equally inclined to each other downwards, cause no deviations in the plane which forms the centre of their lateral distances.

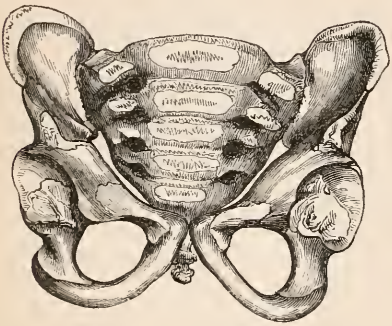
So that the so-called *axis* of the pelvic *cavity* is not one right line, as stated by Müller and Rœderer; nor is it properly expressed by perpendicular lines drawn from three planes, as Levret suggested; nor by a continuous geometric "*arc de cercle*," from the superior to the inferior plane, as G. Bang, Choulaut, Camper, and Carus concluded; nor by the meeting of the axes of the superior and inferior outlet, as is somewhat loosely stated by some more modern writers on obstetrics; but it is a more or less irregular parabolic curve, passing from the fixed axis of the brim, and moveable forwards at its inferior extremity with the moveable axis of the inferior outlet, with which it coincides below.

It may be here added, to prevent misconception, that the line of direction of the inferior outlet is in the living female inclined forwards in a much greater degree (*n*, *b*), than that of the osseous pelvis, by the prolongation of the posterior wall in the soft parts of the perineum.

General Development of the Pelvis. — In common with the inferior extremities, the pelvis, in the infant, is more tardy in arriving at adult perfection than the upper parts of the body; and this delay is more evident in the inferior or true than in the superior pelvis, and considerably facilitates its transit through the maternal structures. *At birth*, the iliac wings are flat, and their surfaces are directed more forwards and less inwards than in the completely formed pelvis. From the narrowness of the sacrum, and the shortness of the pubes, the transverse dimensions of the brim and cavity are very small, and the antero-posterior diameter, from this cause, is larger than the lateral, by $\frac{1}{4}$ to $\frac{1}{2}$ an inch. The shape of the superior opening is less rounded than in the adult, being of a sub-quadrate rather than an oval form. The cotyloid part of the ilia is completely cartilaginous, contracted, and less projecting, while the pubic arch is narrow and angular, and the tuberosities of the ischia are near each other so as to present a small opening at the inferior outlet. Sœmmerring remarks that the obturator foramen is more elliptical in the infant than in the adult. The depth and general appearance of the true pelvis is smaller than is proportionate to the iliac wings; and it is of nearly equal breadth throughout.

The *parallelism* of the lateral, as well as of the anterior and posterior pelvic walls is, I think, sufficiently marked and general to be considered as a characteristic of the conformation of the infant pelvis, as we shall find it to be of that of most of the lower animals, giving to it a square-sidedness which is well seen in the adjoining figure.

Fig. 85.



Pelvis of the Child at birth.

The sacrum and coccyx in the child at birth are much less curved, vertically, than they afterwards become, which causes the posterior wall to be longer than is proportionate. The coccyx, indeed, in many instances I have seen, was almost vertical. The sacro-vertebral angle is consequently much less marked than in the adult. Doubtless, muscular action, increasing as the development of the bones progresses, has a great effect in producing the diminution of the sacro-vertebral angle backwards in after life.

It is commonly stated by anatomists, that the infant pelvis is more obliquely placed on the spinal column than the adult pelvis. The inclination of the superior plane in the child has been placed by the brothers Weber at an angle of 154·66 with the transverse vertical plane. This is somewhat *less* than the inclination in the male, according to the same observers, viz. 155°.

The following table is the result of the measurements of the pelvic angles of five infants, made to ascertain the correctness of this statement. The angles were carefully taken, with much precaution against any abnormal displacement, so readily occurring in the pliant structures of the infant, by making an antero-posterior vertical section of the pelvis and whole spinal column with the whole of the soft parts attached, and in such a manner as would have tended rather to increase, than to diminish, the pelvi-vertebral angle.

	Angles.	
	Pelvi-vertebral.	Sacro-vertebral.
1. Fœtus at 6 months, *female*	150°	155°
2. " " *male* -	150°	145°
3. Infant at full term, 7 days old, *female* - -	150°	145°
4. Infant at full term, *female* - - -	150°	140°
5. Infant at full term, still born, large and well-made, *male* - -	140°	140°

It will be remarked that the greatest difference from the adult is observable in the *sacro-vertebral angle*, which is from 10° to 15° greater than the average female adult, and from 23° to 28° greater than the average male adult.

I should here state, also, that the results of my own measurements of the angle of the superior pelvic plane in adult male subjects, have given somewhat *less* angles than that stated by Weber.

According to Cruveilhier, a horizontal line, from the upper border of the pubis, meets the posterior wall much lower in the infant than in the adult, though the point at which he places it in the adult, viz., a little below the base of the sacrum, is much too high in the natural position of the pelvis, as will be seen by inspection of the diagram (*fig.* 84.). In all the infant pelves I have just given, the tip of the coccyx reached as low as the *lower border* of the symphysis pubis; both these points exactly coinciding with a line drawn perpendicular to the transverse vertical plane. This may, perhaps, be attributed to the greater flatness of the sacro-coccygeal wall in the infant, extending it further downward. In *No.* 5. the male child at full term, the *angle of inclination of the pubic symphysis* to the transverse vertical plane was only 25°, but in the last female child it was, 40°, both being less than the mean adult angle, 50°, before given, and showing, like the *sacro-vertebral* angle, a greater tendency to parallelism with the spine, as in the inferior animals, an analogy which is also seen in the elongated conjugate diameter.

Resulting from this tardy development of the pelvis, the bladder and greatest portion of the rectum, in the child at birth, are contained almost entirely in the abdominal cavity, on a level with the ilia or false pelvis, and only descend gradually afterward into their adult position with the slow development of the pelvic bones, assuming their permanent position about the period of puberty, a circumstance very necessary to be borne in mind in operations on these viscera in children below that age. Hence one cause of the greater prominence of the belly in children from the additional number of its visceral contents.

According to Dupuytren, the female pelvis differs very little from that of the male till puberty, at which period it has a general triangular form in both sexes, but, after that period, it becomes rapidly developed, and soon assumes its distinctive sexual character. The transverse diameters begin to exceed the conjugate, and, in the female, attain a great preponderance, constituting one of the great characteristics of the fully formed human pelvis, as distinguished from that of the lower animals.

In Autenrieth's method of calculating the pelvic dimensions, the dorsal, or posterior part, bears a proportion to the anterior or abdominal part, as 10 to from 11 to 14, in the infant of two years; while, in the adult pelvis, it was as 10 to from 16 to 22.

In *advanced adult age*, the pelvic inclination is said by Cruveilhier to be *increased* in consequence of the forward curvature, or drooping of the spinal column, which tends to arrive at the horizontal position, as in quadrupeds. To keep the centre of gravity between the lower extremities, the femurs, in old persons, are more flexed upon the pelvis, so as to be more directed towards the line of the superior pelvic plane. I have found, however, that in old subjects, although the angle of the pelvic plane with that of the *whole* spinal column is increased, yet the angle with the lumbar vertebræ only, is not so much changed, and that, apparently, the increased muscular traction on the sacrum and posterior part of the ilia by the muscles of the back acting upwards, and of those of the front of the thigh acting downwards, upon the anterior part of the pelvic lever, in order to preserve the erect position, produce this increased obliquity of the pelvis, which is generally accompanied by a corresponding *decrease* of the sacro-vertebral angle. This will be more fully comprehended when considering the mechanism of the pelvis.

Muscular Attachments of the Pelvis. — To afford a fixed point for the attachment of the numerous and powerful muscles acting on the trunk and extremities is one of the important offices of the pelvis. These may be classed as *posterior spinal* and *abdominal* groups acting on the trunk and spinal column; *extensor*, *flexor*, *adductor*, *abductor*, and *rotator groups* acting on the lower extremity; and *perineal groups* forming the moveable floor of the pelvis and acting on the genital and excretory organs.

1. *Muscles acting on the trunk and spine.*— The *posterior spinal group.*—The *longissimus dorsi* and *multifidus spinæ*, to the upper part of the posterior surface of the sacrum; the *interspinales*, to the superior border of the sacral crest; and, according to some, the *extensor coccygis*, to the contiguous posterior surfaces of the sacrum and coccyx; the *sacro-lumbalis*, to the middle part of the posterior third of the iliac crest, and to the contiguous sacral surface; and the *latissimus dorsi*, through the lumbar fascia to the external lip of the posterior half of the iliac crest and to the sacral crest. This muscle acts on the arm. The *abdominal group.* — The *obliquus externus* and *internus*, and *transversalis abdominis*, to the external lip, middle ridge, and internal lips respectively of the iliac crest, and also by their aponeurotic tendons to the angle, crest, spine, and pectineal line of the pubis (the external oblique tendon, under the name of Poupart's ligament, stretching across, from the anterior superior iliac spine to the spine of the pubis, and, under the name of Gimbernat's ligament, passing backwards to the linea-ilio pectinea; and the internal oblique and transversalis tendons enclosing the rectus abdominis muscle, and uniting to form the conjoined tendon); the *quadratus lumborum*, to the posterior fourth of the inner lip of the iliac crest; the *rectus* and *pyramidalis abdominis*, to the crest of the pubis; and the *psoas parvus*, when present, to the pectineal eminence.

2. *Muscles acting on the leg.* — The *flexor group.*—The *rectus femoris*, to the anterior inferior iliac spine and outer part of the cotyloid rim; the *iliacus*, to the whole anterior concave surface of the iliac wing — the *psoas magnus* is not attached to the pelvis, but acts upon it by passing over it along the pelvic brim; and the *sartorius*, to the anterior superior iliac spine and notch below it.

The *extensor group.* — The *biceps flexor cruris*, *semitendinosus*, and *semimembranosus*, to the depending middle and posterior parts of the ischial tuberosity; and the *gluteus maximus*, to the quadrilateral gluteal impression on the dorsum of the ilium, to the posterior surfaces of the two lower pieces of the sacrum, and of the two or three upper pieces of the coccyx, to the oblique sacro-iliac and great sacro-sciatic ligaments, and to the lumbar fascia.

The *adductor group.*—The *adductor magnus*, to the anterior part of the ischial tuberosity, and to the united ischio-pubic rami; the *adductor longus*, to the anterior surface of the angle of the pubis; the *adductor brevis* below the foregoing, to the same surface; the *pectineus*, to the spine, pectineal line, and horizontal ramus of the pubis; and the *gracilis*, to the rough internal border of the ischio-pubic rami and symphysis pubis.

The *abductor group.*— The *gluteus medius*, to the dorsum of the ilium, between the crest and superior curved line; the *gluteus minimus*, to the same surface between the curved lines; and the *tensor vaginæ femoris*, to the outer surface of the anterior superior iliac spine.

The *rotator group.*—The *pyriformis*, to the anterior surface of the sacrum between the four upper sacral holes, and passing out through the great sciatic notch; the *obturator externus*, to the inner half of the external circumference of the obturator foramen, and to the external surface of the membrane closing it; the *obturator internus*, to the internal surface of the same ligament, and to the borders of the foramen, and also to the surface of bone opposite the cotyloid cavity (this muscle passes out through the small sciatic notch, over which it is bent as over a pulley); the *gemellus superior*, to the outer surface of the ischiadic spine; the *gemellus inferior*, to the posterior extremity of the ischiadic tuberosity; and the *quadratus femoris*, to the external border of the same tuberosity.

3. *Muscles acting on the perineum and genitals.*—The *posterior perineal group*. The *levator ani*, to the middle of the inner surface of the symphysis pubis, to the inner surface of the ischiadic spine, and to the tip of the coccyx; the *ischio-coccygeus*, to the same inner surface of the ischiadic spine, to the lateral border of the coccyx, and to the inner surface of the small sacro-sciatic ligament; and the *sphincter ani*, to the tip of the coccyx.

The *anterior perineal group*.—The *transversus perinei*, to the middle of the inner border of the ischial tuberosity; the *accelerator urinæ* (or, in the female, the *sphincter vaginæ*), to the anterior part of the inner border of the ischial tuberosity; the *erector penis* (or, in the female, *clitoridis*), to the ascending ramus of the ischium; and the *compressores urethræ*, to the descending ramus of the pubis, and to the sub-pubic ligament.

Fascial Attachments.—Besides the foregoing, the pelvis also affords attachment to many important *fasciæ*, which are susceptible of division into *lumbar*, *abdominal*, *crural*, *pelvic*, and *perineal*.

The *lumbar fascia* is formed by the junction of the tendon of the latissimus dorsi muscle with the fascia vertebralis, and the united posterior tendons of the internal oblique and external division of the transversalis tendon, and it is attached along the sacral crest and posterior surface of the fourth sacral bone, and to the posterior half of the iliac crest, enclosing the sacro-lumbalis muscle.

The *abdominal fasciæ* are three in number, viz., the *fasciæ transversalis*, attached along the inner lip of the iliac crest, to Poupart's ligament, and to the crest, spine, and pectineal line of the pubis; the *fascia of the quadratus lumborum muscle*, or anterior division of the tendon of the transversalis, attached to the inner lip of the posterior fourth of the iliac crest, and to the ilio-lumbar ligament; and the *iliac fascia*, attached to the ilio-lumbar ligament, along the inner margin of the iliac crest, and to the anterior superior iliac spine.

The *crural fascia* or *fascia lata* is divided into three portions, named, from their respective attachments to the three portions of the innominate bone, *iliac*, *pubic*, and *ischiadic*. The outer lip of the iliac crest, the anterior superior spine, and Poupart's ligament, give attachment to the *iliac* portion, which separates the lateral abdominal from the external leg muscles; the spine, crest, angle, pectineal line, and descending ramus of the pubis, to the *pubic* portion, which separates the internal leg muscles from the anterior abdominal and anterior perineal group of muscles; and the tuberosity and ascending ramus of the ischium to the *ischiadic* portion, which separates the posterior leg muscles from the posterior muscles of the perineal group.

The *pelvic fascia* is composed of two portions, the *recto-vesical* and *obturator*, which, having a common attachment to the anterior surface and promontory of the sacrum, to the anterior and lateral parts of the pelvic brim, and to the iliac fascia, separate opposite the line of origin of the levator ani muscle, which arises between them, from the symphysis pubis to the ischiadic spine. The *obturator* division is attached to the inner margins of the ischiadic tuberosity and ischio-pubic rami, being connected with the falciform margin of the great sacro-sciatic ligament behind, and secluding the obturator muscle from the ischio-rectal fossa; the *recto-vesical* division, forming the anterior and lateral true ligaments of the bladder, is attached to the posterior surface of the symphysis pubis above the origin of the levator ani, and to the inner surface of the ischiadic spine.

The *perineal fascia* is divided into two portions, *deep* and *superficial*, which enclose between them the superficial muscles of the anterior perineal group, and also the bulb of the urethra and the crura of the penis. The *deep perineal fascia* or *triangular ligament* is subdivided into two layers, anterior and posterior, which enclose between them the membranous urethra, with its compressor muscles and Cowper's glands. They are both attached to the lower border of the pubic symphysis and sub-pubic ligament, and to the inner border of the united ischio-pubic rami, and intervene between the posterior and anterior perineal groups of muscles. The *superficial perineal fascia* covers in the anterior perineal region, and is attached to the anterior part of the inner border of the ischio-pubic rami, and to the anterior surface of the angle of the pubis.

The *crura of the penis*, or, in the female, those of the *clitoris*, may also be mentioned as implanted on the rough inner border of the ischio-pubic rami about their junction; as well as the *round uterine ligament*, in the female, to the anterior surface of the pubis.

Mechanics of the Human Pelvis.—When we consider the pelvis with regard to its architectural adaptations, and compare it with the principles of engineering, we are struck with the beautiful simplicity of the means by which it combines strength with elasticity, and lightness with capacity and unity of design. The weight of the trunk is to be transmitted through the lumbar vertebræ to the sacrum, and from thence to points of support, which vary with the position of the inferior extremities. In the erect position, these points are the femora. In the sitting position they are the tuberosities of the ischia.

The experiments of Weber have proved that though the centre of gravity of the *trunk* itself (without the legs) is placed in the transverse vertical plane as high as the sterno-xiphoid joint, yet the centre of gravity of the *whole body*, as marked by the point of section of the before-mentioned transverse-vertical with a horizontal plane, is placed only

8·7 millimetres above the sacro-lumbar joint, or just above the pelvic arch. All weight on the arch, such as that of the trunk, is supported most easily when its line of gravity falls through this part, and coincides with that of the whole body in the transverse vertical plane, and the trunk will be found to be thrown into such a position, when supporting heavy weights, as will tend to produce this effect. And, according to the researches of Rokitanski, when the sacro-vertebral angle and pelvic inclination is increased, as by hip disease, there is always a compensatory curve of the spine backward, to keep the centre of gravity above this point.

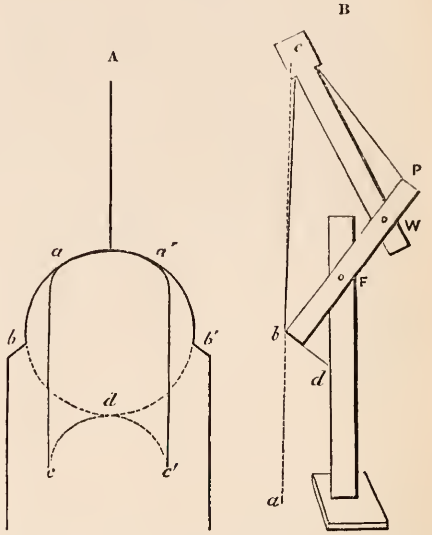
In artificial constructions for the purpose of transmitting a weight downwards from a central to two lateral points, a segment of a circle, or *arch* is most commonly made use of, and generally consists of two lateral curved portions, composed of separate parts or *voussoirs*, with an interposed substance between them called a *keystone* or crown-piece, of a wedge shape, and placed with the broad end uppermost. This wedge shape exactly corresponds to the interval which would be left between the lateral curved pieces, having their ends cut square. Any force operating on the keystone from above tends only to drive the broader part of the wedge further between the lateral pieces, at the same time pressing them nearer to each other, and so to increase the firmness of the arch, so long as the extremities are firmly fixed in the ground and prevented from starting outwards, which is generally accomplished by means of abutments.

Constructed upon this plan, the pelvis presents two lateral curved thickened buttresses or columns, passing from the cotyloid to the sacro-iliac articulations, and two others passing on a plane posterior to these from the tuberosities of the ischia along their descending rami, and through the ilia to the same sacro-iliac articulations; and interposed between each of these corresponding lateral pieces is the common keystone of both the arches thus formed, the wedge-shaped sacrum.

The sacrum thus forms the common culminating point of two arches, viz., the *cotylo-sacral* or *standing arch*, and the *ischio-sacral* or *sitting arch*. And the planes of these two arches are so directed as to coincide or become applied to each other at the top of the great sciatic notch, as may be seen by reference to the diagram (*fig.* 86. A, *a a′*). In this comparison, however, it must be borne in mind, that the extreme tenacity and strength of the material used, *bone*, obviates the necessity of the use of many pieces in the lateral portions, such as the "voussoirs" of stone arches, and is more analogous to the iron materials sometimes used for this purpose. And it is in these lines of pressure that we find the bulk and strength of the osseous structure of the pelvis most displayed.

The span of the cotylo-sacral arch being greater, and more elliptical in the female than in the male, where it is almost circular, renders them less able to support heavy weights; and on account of the greater distance to

Fig. 86.



A, *diagram of the pelvic arches:*—*b, a, b′*, cotylo-sacral arch; *c, a, c′*, ischio-sacral arch; *b, d, b′*, cotylo-pubic tie; *c, d, c′*, ischio-pubic tie.
B, *diagram of pelvic levers*:—*c, a*, line of gravity; F, *b*, pubic lever; F, W, cotylo-sacral lever; W, P, posterior spinal or iliac lever; P, *c*, direction of spinal power; W, *c*, direction of spinal weight; F, cotyloid fulcrum; *d*, femoral support.

which it separates the femurs, contributes to produce the waddling gait in running which is characteristic of this method of female progression.

Instead of abutments to prevent the extremities of the arch starting outwards, we often see, in artificial constructions, a connecting link or *tie* extending between these extremities to hold them together, or the circle of which the arch is a segment is completed below, as in tunneling.

Such a tie and completion of the circle we have in the horizontal rami of the pubic bones, for the cotylo-sacral arch, and in the united ischio-pubic rami, for the ischio-sacral arch; and they are connected in front, at the pubic symphysis, exactly as these two arches themselves are behind at the sacro-iliac joints.

By the vertical *ischio-pubic arch* thus formed, that portion of the pressure which has a tendency to push forward and upward the extremities of the ischio-sacral arch, is supported and thrown upon the cotylo-sacral arch, the whole weight of the trunk, in a sitting posture, being thus divided between them The ischio-pubic rami are the parts of the pelvis most liable to fracture, according to Cruveilhier, from the application of force acting on the ischia.

The *cotylo-pubic arch* not only resists the starting outward of the ends of the cotylo-sacral arch, but it resists their displacement inwards, which would result from the pressure of the femora in the direction of the necks of these bones. The effect of this pressure, when the pubes yield to it, is shown in the deformity which has been termed the *rostrated pelvis*, resulting from the crushing of these bones together. The cotylo-pubic arch also receives, in its concavity, part of the weight of the abdominal viscera, though, from the attachment of these to the spine, their chief weight is concentrated upon the common centre of pelvic arches,—the sacrum. The ilia are also generally supposed to support the intestines in a great measure; but this support, on account of their great obliquity in the erect position, cannot be so important as is commonly imagined, except, as in the case of the cœcum and rectum, through peritoneal attachments. The human pelvis, when thus taken in conjunction with the thorax, forms the base of a cone, the apex of which is the neck, a disposition for supporting the contained viscera which the erect position demands, and which contrasts strongly with the structure of quadrupeds.

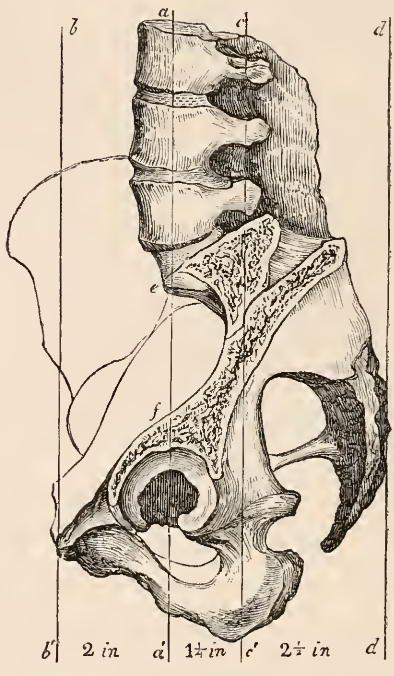
Again, the cotylo-sacral and pubic arches on each side, united at their extremities in the acetabula, form *two lateral arches*, on the centres of which rest the thigh bones. Against the lateral pressure exercised by the thigh bones, these two arches, connected, at their anterior and posterior extremities, by the symphysis pubis and sacrum, form, as Mayo observes, an elastic hoop. The ischia also contribute to this resistance against lateral pressure, and form, with the two other portions of the innominate bones, a sort of arched tripod, on the apex of which the femur is supported.

In addition to the buttresses already described, there is, placed vertically above the cotyloid cavity, a thick *rib* of bone, which transmits to the arched crest of the ilium, and through it and the sacro-iliac joint to the sacrum, a portion of the direct vertical pressure from the heads of the thigh bones. This thickened portion of the iliac wing has been mentioned in the general description of the bone as impinging on the iliac crest in the middle of its anterior curve. The division of the pressure thus produced, no doubt calls into action much more completely the elastic resistance of the pelvis, in sudden increase of weight. Thus in the sacro-iliac joint meet three buttresses or thickened lines of pressure, of which the *direct cotylo-sacral* is the central and principal one, the *ischio-sacral* the lowest and next in strength, and the *superior* or *indirect cotylo-sacral* the weakest.

But, besides merely supporting quiescent superincumbent weight, the pelvic arches are required to resist and break the force of shocks and concussions meeting with the inertia of the trunk, and passing from the lower extremities of the body to the vital and delicate cranial and thoracic structures. These dynamic requirements are met by peculiar modifications of the simple arch, combining with it, by an admirable adaptation, the qualities of an elastic spring.

First, the cotylo-sacral arch, on which the greatest number and force of shocks falls, is not placed *vertically*, but *obliquely upwards* and *backwards*, while the cotylo-pubic arch, being united to it at its extremities, and continued in the same plane over the femoral supports, forms the anterior arm of a bent lever of the first order, of which the cotylo-sacral arch is the posterior curved arm, the spinal column the weight, and the heads of the femurs the fulcrum (see *figs.* 87. and 86. B).

Fig. 87.



Drawing of a section of the pelvis in the cotylo-sacral arch, removing the left iliac wing. a, a′, line of *fulcrum* falling in the transverse vertical plane of trunk; c, c′, line of *weight* passing through centre of sacro-iliac joint; b, b′, line of *power* or pubic projection; d, d′, line of sacral projection; e, f, cotylo-sacral curve; a′, b′, pubic arm of lever; a′, c′, cotylo-sacral arm; a′, d′, length of gluteal arm; c′, d′, posterior spinal arm; g, posterior iliac projection.

The anterior or pubic arm of this lever giving insertion to the powerful extensor muscles of the thigh, which represent the *power*, is thrown upwards by the operation of downward force on the crown of the cotylo-sacral arch, calling these muscles into contractile reaction, which overcomes gradually the force of any shock operating at the posterior extremity of the pelvic lever over the fulcrum of the thigh bones. In well-formed male pelves, the pubic arm of this lever is increased in power by being longer than the cotylo-sacral by $\frac{1}{2}$ or $\frac{3}{4}$ of an inch, the one being 2 inches, the other $1\frac{1}{4}$ inch, in direct distance from the centre of the cotyloid support (*fig.* 87. *a′ b′*, *a′ c′*).* This gives the anterior muscles of the thigh greater power in resisting the downward force of the trunk at the sacral extremity of the lever.

But by the addition of the iliac and sacral projections posteriorly, the cotylo-sacral arm is increased in length by 2½ inches, as will be observed on reference to the figure (*c′*, *d′*), a disposition which evidently increases the power of the glutei muscles in maintaining the habitual erect position, and resisting any tendency to fall forwards, by extending the femora on the pelvis.

Again, if we follow the lateral curve of the sacrum at the brim of the pelvis, we shall find that it projects forward in the promontory of the sacrum, immediately under the point supporting the spine, so that its profile, taken with that of the ilium, as seen in the figure (*c f*), presents a curve with the concavity forward, in the manner of a C spring. It is worthy of remark, that, in the erect position, a plumb line, dropped opposite to the centres of the bodies of the axis and last lumbar vertebra, passes across the centre of the sacral promontory, and directly between the centres of the cotyloid cavities, as was proved by the experiments of Weber. Such a plumb line marks exactly the line of the transverse vertical plane of the spinal column before mentioned, which, when continued downwards, passes through the *sacral extremity* of the pelvic lever, and also through the *cotyloid fulcrum*, dividing equally and vertically the heads of the thigh bones, and crossing the ischio-pubic rami about their suture (*a a′*). Thus, the oblique C-like curve of the cotylo-sacral arch, or posterior bent arm of the lever, meets this plane at its two extremities, directing its concavity towards it like the arc of a circle to its chord; and contributes, by its elastic reaction, to break the force of shocks operating through the spine and femora. In deformed pelves, we generally find that the sinking of the sacrum, the crown of the pelvic arch, under the weight of the trunk, produces an increased curvature of the iliac bones *forwards* by the yielding of the C spring, and thus still further encroaches upon the dimensions of the pelvic brim.

The above considerations will illustrate the fallacy of the deduction of Cruveilhier in respect to the *statics* of the pelvis. This celebrated anatomist remarks, that "the articulation of the vertebral column with the pelvis is situated at the back part of that cavity, while the articulation of the femurs is anterior and lateral. The distance between them increases the space in which the centre of gravity can oscillate, without being carried so far forward as to pass beyond a perpendicular, from the cotyloid cavity to the base of support at the feet" (p. 514. vol. i. *Anat. Descrip.*). Now these experiments of Weber prove that the centre of gravity is directly *over* the cotyloid support, and cannot oscillate between these two articulations. The only oscillation of the line of gravity which can take place without falling is along the length of the basis of support — the feet.

Soon after, in reference to the sitting position, he says, "the tuberosities of the ischia being a *little anterior* to the cotyloid cavities, and *near the front of the pelvis*, the centre of gravity tends to pass behind the base of support; and the body easily falls backward in that position." Now, the tuberosities of the ischia, in the erect posture, are considerably *behind* the line of gravity, or transverse vertical plane, which crosses at or near the ischio-pubic ramal suture; and though, in the sitting posture, they are brought a little nearer the line of gravity, yet a much more satisfactory reason of the trunk more easily falling backwards than forwards, is because of the support of the hams in front, and the elevation of the coccyx behind above the plane of support.

Again, by the projection of the sacrum and tuberosities of the ilia behind the sacro-iliac joints, another lever, less powerful than the foregoing, is formed, having also the cotylo-femoral supports for its fulcrum, and the spinal column for its weight, the anterior arm of this lever being the cotylo-sacral arch (*fig.* 87. *a′*, *c′*), and the posterior, the overhanging tuberosities of the ilia and projecting sacrum (*c′*, *d′*). Measuring from the centre of the sacro-iliac articulation, the anterior arm is 1½ inch in direct length, and the posterior about 2 inches and a half. The power in this lever resides in the powerful muscles which pass from the sacral and iliac bones posterior to the sacro-iliac joint, to the osseous spinal projections and appendages above—viz. the longissimus dorsi and sacro-lumbalis, and its action is shown in the increase of the pelvic inclination on the change from the sitting to the standing position; the principal movement taking place in the sacro-lumbar joint. It acts to the most advantage when the *centre of gravity* of the *trunk*, from which it is derived, is thrown *in advance* of the cotyloid fulcrum (*a a′*), so that the lever, though apparently one of the second order (i. e. in which P and W are on the same side of the fulcrum), is in reality one of the first order, [in which the fulcrum may be between them, and supports both the power, P, and the weight, W. Hence, in the drooping of the trunk forwards in old age, the action of these muscles contributes, to produce the increased obliquity of the pelvic lever in the manner before described. This may be made more evident by inspection of the diagram (*fig.* 86. B), which is taken from a small brass model made to illustrate this point. It will be seen that the pressure on the cotyloid fulcrum, F, could not be W − P, as in the second order of levers, but must necessarily be W + P, and therefore in the first order of levers. P, in this case, may be represented

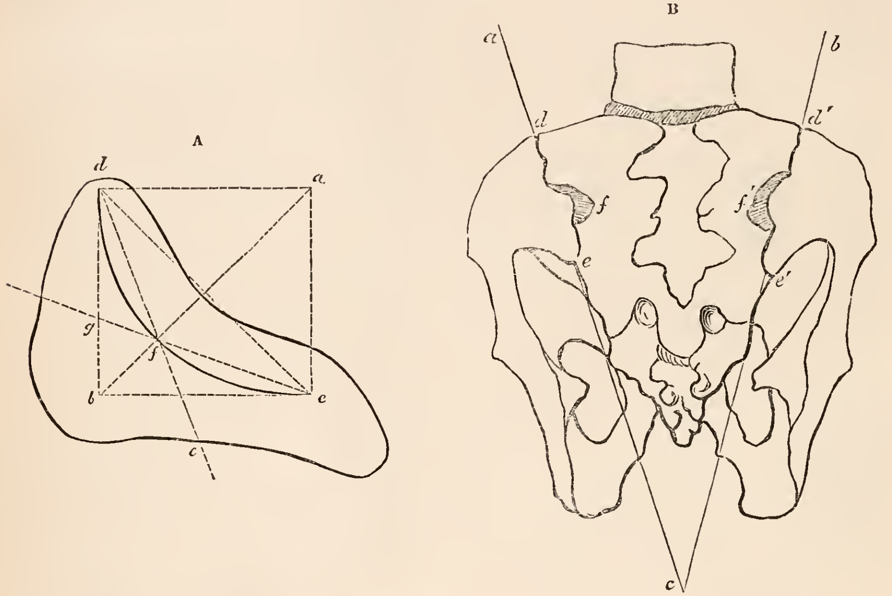
* The line *c c′*, in the diagram passes through the centre of the sacro-iliac joint,—at which point, a line drawn from the cotyloid fulcrum of the bent lever falls perpendicularly upon the line of action of the weight, transmitted obliquely in the sacral axis, — and this consequently, the effective point of power of the bent arm *f. e.*

by the line P *c*, and the line of gravity of the trunk, *c a*, and is doubtless considerably increased by the resisting tension of the anterior abdominal muscles acting through the extensors of the thigh on the femoral supports in the line *c b*, *b d*.

In the foregoing dispositions of the pelvic structure, the office fulfilled by the *sacrum* is so compendious and important as to call for particular attention to the shape and position of that bone, and the manner in which it is articulated with the ilia, so as to be at once firm and strong as a keystone, yielding as a spring, and moveable as a jointed bone. And we shall find all these requirements beautifully provided for.

First. The sacrum is wedge-shaped, when viewed at its anterior aspect, narrowing from *above downward*, especially along the surface immediately between the lower portions of its iliac articular surfaces in the plane *b*, *e* (*fig.* 88. A), which are inclined to each other at an angle varying from 15° to 30°, and averaging about 20°. When viewed from above at its base, as in *fig.* 89. *page* 144.), it also presents a wedge shape with the base directed *anteriorly*, the lateral masses of the base becoming narrower from *before backwards;* so that the

Fig. 88.



A, *diagram of the sacral auricular facet, natural size and placed as in the erect position of the body, with the lines of tension and pressure.* *a*, centre of action of the posterior deep ligaments; *d f e*, arc of sacral groove, forming a quadrant with the lines of tension, *a d*, *a e*; *d e*, chord of the arc; *d f*, *e f*, chords of the semi-arcs; *d g e*, sacro-vertebral angle; *d b e*, triangle forming the sacral "voussoir;" *b* and *e*, position of sacral "joggles."

B, *diagram of a transverse section of the pelvis in the line of the sacral axis, posterior view*; *a c b*, angle of vertical sacral wedge; *d*, *e*, depth of sacro-iliac articulations; *f*, interosseous sacro-iliac ligaments.

sacrum appears to be a double wedge, having its broadest part at the border of junction of the base with the anterior surface, and tapering from this point, both upwards and backwards and downwards and backwards.

Hence it has been stated by Cruveilhier to be liable to dislocation downwards and forwards, from the want of bony support in that direction. But the sacrum, in the erect position of the body, is placed, not vertically, but obliquely, with its base directed more forwards than upwards, and its anterior surface more downwards than forwards, so that the upper limb of the auricular surface is placed nearly vertically, and the lower nearly horizontally, as seen in *fig.* 88. A. The diminished breadth of the base of the sacrum posteriorly is due to the bevelling of the lateral surfaces for the implantation of the deep posterior and interosseous ligaments, as seen in fig. 88. (B, *e*), the bone not being here in apposition with the overhanging iliac tuberosities, — the area of absolute contact being confined to the auricular surfaces themselves. Again, the increased breadth of the anterior surface at the auricular angle *c* (*fig.* 89.), will be found, on careful inspection, to depend upon the presence of the pointed projections on each side, before described as received into corresponding depressions on the auricular surfaces of the ilia, which latter, being circumscribed below by a raised border, cause the sacrum to *bite* on the ilia here to a considerable extent, forming what is called, in engineering nomenclature, a "joggle" to the sacral "voussoir." By the iliac support thus received, the position of the sacrum is well protected against pressures, coming either directly downwards in the line *d*, *b* (*fig.* 86. A), or downwards and forwards in the direction of the line *a*, *b*; *b* being placed in the diagram upon the sacral projection. By measuring in eight sacra, the distances between the upper extremities of the auricular facets on each side, at the point *d*, marking them off on paper, and then taking the distances in like manner at *c*, which corresponds to the lateral notch opposite the second sacral vertebra (*see fig.* 78. A, *b*.), I found the line *d*, *c* to coincide pretty nearly with the mean direction of the superior vertical limb, and with the superior half of the central curved groove *d*, *e*; and to fall in a plane which was inclined to the one on the opposite side, so as to form with it an angle varying from 15° to 25°, and in all cases directed *downwards*.

Now, the sacrum is so placed in regard to the cotylo-sacral arch, and the line of pressure from above, that the angle formed by the surfaces of the base and anterior face is the narrowest point of a rapidly-expanding articular wedge placed antero-posteriorly. This is better seen by a lateral view of the auricular facet, with the bone in the natural oblique position, as in *fig*. 88. A. The facet will then be seen to have its angular projection pointing downwards and forwards in the direction of the cotylo-sacral arch in the line *a b*, and its two limbs diverging so as to present a broad surface of articulation with the ilia in the lines *b d*, *b e*, forming with *d e*, the triangular "voussoir" *d b e*. The depth of the keystone is the greatest distance between the anterior border of the superior limb, *d*, and the inferior extremity of inferior limb, *e* (*fig*. B), and is about $2\frac{1}{2}$ inches in the adult male. The wedge shape formed by them is well seen in the posterior view of a transverse section along the sacral axis, as in *fig*. B, where the lines *a c*, *b c* show the obliquity of the wedge, and form an angle *a c b*, of from 20° to 35°. In a direction downwards and *backwards*, then, the sacrum has, like an artificial "voussoir," or keystone, its broad end directed *upwards* towards the point of pressure.

But, as Cruveilhier has justly observed, forces acting in the curve of the lumbar vertebræ are partly counteracted by the elastic spring-like yielding of the lumbar and sacro-lumbar fibro cartilages; and by the lumbar curve they are, at the same time, directed *backwards* as well as downwards (viz., — at first in the direction of the line *d*, *f* (*fig*. 88. A), and then in that of *f*, *e*, which latter, produced to meet the vertical line *d*, *b*, at *g*, forms an angle *d g e*, of about 117°, *coinciding* with the average *sacro-vertebral* angle *in the direction of the sacral axis*), — thus tending to drive the broad end of the sacral "voussoir" between the narrower iliac intervals; and so, in relation to the direction of the *principal* forces acting on the pelvic arch, the sacrum becomes a true keystone.

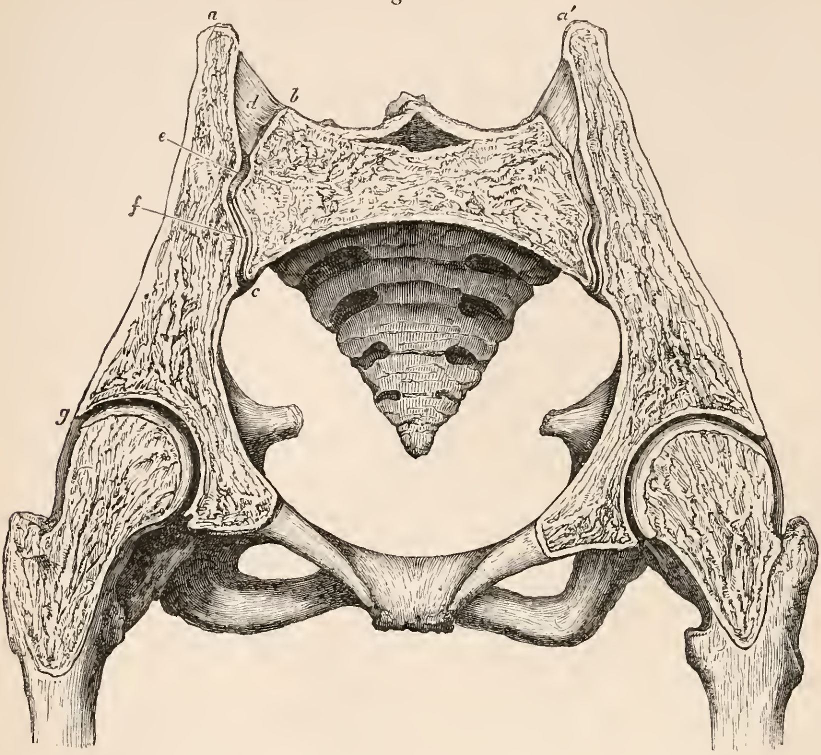
Another arrangement which would tend, from the obliquity of the bone, to counteract any forward displacement, is the sudden inversion of the vertical sacral wedge at the extremity of the lower limb of the auricular surface (*fig*. B, *e*), opposite the third sacral bone, at which point, we have mentioned in the description of the sacrum, the anterior surface becomes suddenly broader from above downwards; so that here the sacrum by another "joggle" again *bites* on the iliac. A third disposition preventive of this displacement has been pointed out by Mr. Ward, in the superiority of breadth of the posterior over the anterior surface of the sacrum, opposite the point *c*. (*fig*. A.), the middle of the inferior articular limb in many instances.

Behind and above the angular projection on the sacral facet is an elongated depression or *groove*, which passes along the centre of both limbs of the auricular surface, and receives a reciprocal elevation on the *iliac* articular surface (*fig*. 89. *f*.) Now this ridge on the iliac surface evidently bites in its turn on the sacrum, and presents another obstacle to anterior displacement in the superior limb, as well as to downward displacement at the inferior limb. The surfaces thus applied to each other, being so curved, *give a greater extent of apposition* than if they were plane, and, at the same time that they allow of a limited yielding of the sacrum to pressure, keep the surfaces continually in contact. And we shall find that, although the general shape of the articular surface is rendered angular by the "joggle" *b* (*fig*. 88. A), the groove and corresponding iliac ridge form a regular crescentic curve, or segment of a circle *d*, *f*, *e*, of which, in fact, the central internal projection of the tuberosity of the ilium above at *a* is the centre. Now it is to this prominence that the powerful deep posterior and interosseous sacro-iliac ligaments are mainly fixed above; and it is by being suspended by and moving on them in the radius *a*, *f*, that the sacrum slides on the ilia downwards and backwards in the direction of this groove on the reception of force from above.

That this motion, though limited, does take place, and in this direction, may very readily be proved, on the detached pelvis, by striking directly downwards on the upper extremity of three or four lumbar vertebræ cut off with it. The impulse will be almost entirely felt at the tip of the coccyx, in a direction upwards and backwards. That portion of it which is directed immediately downwards is checked by the powerful ligaments above mentioned, and is but little felt at the sacral promontory.

If a section of the whole pelvis, in the direction of the cotylo-sacral arch is made, as in the next figure, a very important element in the mechanism of the sacro-iliac articulation is brought to view; viz., the deep posterior and interosseous sacro-iliac ligaments, (*d*, *c*.) These ligaments are continuous one into the other, becoming shorter downwards, as the distance between the bones becomes less. They narrow also antero-posteriorly, so as finally to be received into the retiring angle formed by the limbs of the articular facet, at which point they are seen in the transverse section in the sacral axis in *fig*. 88. B, *f*. They are attached, externally, to the central prominence on the inner surface of the iliac tuberosities, *a*, *a′*, which project upwards and backwards, and are curved also a little outwards, the better to resist inward traction,

Fig. 89.

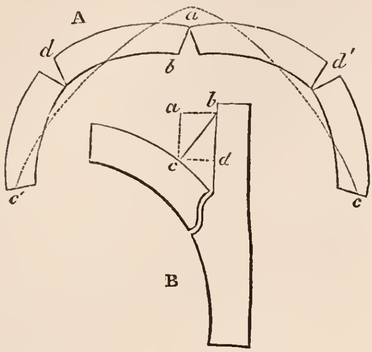


Section of the pelvis and heads of the thigh bones, made in the direction of the cotylo-sacral arch, a little below the pelvic brim; showing the antero-posterior sacral wedge, the suspending office and oblique direction of the posterior sacro-iliac ligaments, and the wavy section of the joint. *a*, iliac tuberosities; *b*, *c*, antero-posterior sacral wedge; *d*, deep posterior sacro-iliac ligaments; *e*, interosseous ligaments; *f*, auricular groove; *c*, sacral joggle; *g*, *c*, cotylo-sacral rib. (Drawing made from a recent section.)

following the lesser curve of the iliac crest. This thickened central portion of the tuberosities is placed above the angle of the articular facet, in the line of direction of the cotylo-sacral arch produced upwards through it. In the accompanying figure, the section, made almost in the plane of the pelvic brim, cuts directly through it. Passing downwards and inwards, the powerful fibres of these ligaments are attached to the upper external part of the posterior surface of the sacrum, *b*; and they suspend the sacrum between them somewhat in the manner of a suspension bridge, of which the iliac tuberosities are the suspending buttresses. This arrangement evidently considerably adds to the yielding elasticity of the sacro-iliac joint, and does much to lessen the concussions passing through it. It is evident also that it is in these ligaments that the most powerful preventive to *anterior* and *downward* displacement of the sacrum resides; for this could not take place without absolute rupture of their numerous fibres, resisting, as they do, all motion of the sacrum, except, in the limited sweep of the radii they form, a motion which exactly coincides with the mover ent of the sacrum proved by the experiment just mentioned.

But these ligaments, from their oblique direction inwards, at the same time that they resist downward pressure, pull with a corresponding force the sacrum and the ilia more closely together, and render, by this constantly tightening and bracing process, all the before-mentioned provisions for resisting displacement more effective, and, by a gradually increasing resistance, overcome the impelling force. To illustrate this effect, it may be mentioned that the effect of placing too much weight on the crown of an artificial arch is to cause the line of pressure (*c*, *a*, *c*, *fig*. 90. A), which ought to pass through the centres of the "voussoirs" perpendicular to their joints, to rise above the "*extrados*" at the apex, *a*, and to be brought within the inner surface or "*intrados*" of the arch, *b*, on each side; and this causes the voussoirs, *a d*, *d c*, to turn on each other at the edges nearest the line of pressure; and in consequence the crown of the arch sinks and opens below, *b*, and the haunches rise and open above, *d*, *d*. The sacro-iliac joints, being the haunches of

Fig. 90.



A, *diagram of a yielding arch.* *a*, extrados; *b*, intrados; *d*, *d′*, the haunches; *c*, *a*, *c′*, dotted line of pressure.

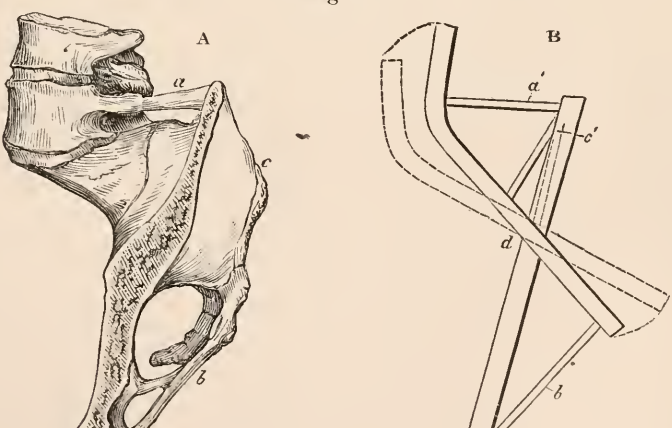
B, *parallelogram of forces of sacro-iliac posterior deep ligaments.* *a*, *c*, vertical or sustaining force; *c*, *d*, lateral or tightening force; *b*, *c*, diagonal direction of ligaments.

the cotylo-sacral arch, have in like manner a tendency to separate above and behind when the pressure on the sacrum is increased; and this tendency is counteracted by the strong posterior sacro-iliac ligaments. By the law of the resolution of forces, this tightening action of the sacro-iliac ligaments may be expressed by the opposite sides, *a b*, *c d*, of a parallelogram (*fig.* B), of which the line of direction of the ligaments, *b*, *c*, forms the diagonal, and the remaining sides, *a c*, *b d*, the sustaining power.

Lastly. Because of the oblique position of the sacrum with regard to the ilia, forces acting on the lumbar vertebræ have a tendency to throw the base or sacral promontory *downwards*, and to tilt the apex with the coccyx *upwards*, as is seen in the experiment of striking the separated extremity of the lumbar vertebræ before alluded to, by the impulse felt at the sacral promontory. It will be better understood by reference to the drawing and diagram of a model made to represent the action (*fig.* 91. A. and B). The tendency of the sacrum is to *turn round* the axis of the sacro-iliac joints in the curve *d f c*, (*fig.* 88. A.), and round the centre *a* (*fig.* 91. *c′*). To counteract this tendency of the base downwards and forwards, the strong *ilio-lumbar ligaments* (*a*) pass backwards and outwards from the last lumbar vertebra to the crest of the ilium, upon which it obtains a long and broad hold. And to resist the tilting upwards of the apex of the sacrum, are attached the extremely powerful *sacro-sciatic ligaments* (*b*), which aid also the *oblique sacro-iliac ligaments* to resist backward displacement.

Thus are constituted two strong yet elastic springs on each side acting upon the *concavities* of the lumbar and sacral curves, which have, perhaps, the most powerful influence of any that have been before mentioned, in breaking the force of shocks and concussions passing along the bones of the trunk and lower extremities. The importance of this office of the sacro-sciatic ligaments is seen in their great strength, and in the consolidation of the lower sacral vertebræ to which they are attached. The forward direction of the base of the sacral wedge when taken antero-posteriorly, as seen by looking from above, facilitates this elastic yielding of the sacral spring, as it evidently could not take place if

Fig. 91.



A, *vertical section of the os innominatum, with the sacrum and ligaments attached,* made in the line of the ischio-sacral support. *a*, ilio-lumbar ligament; *b*, sacro-sciatic ligaments; *c*, iliac tuberosity. (Drawn from a recent section.)

B, *model of the mechanism of the same structures.* *c′*, *d* represents the yielding motion of the posterior deep sacro-iliac ligaments.

the double sacral wedge had a small diameter directed *forwards* as well as *downwards*, in which case it would be prevented by the ilia from moving in that direction at all.

Thus the pelvic supports of the trunk are a peculiar and admirable combination of *the arch* and the *suspension bridge*. Under heavy weights, the preparatory tension of the pelvic muscles, as the psoæ, pyriformes, and great glutei, will, by more closely approximating the sacrum and ilia, produce the conditions of the arch. But in sudden shocks, the strain will fall more immediately upon the ligamentous suspensory structures, as the *sacro-iliac*, *sacro-sciatic*, and *ilio-lumbar* ligaments, more calculated, by their resiliency, to break their force gradually, and finally overcome them.

The thick, strong, and elastic fibro-cartilaginous pads inserted between the opposing osseous surfaces of the sacro-iliac and pubic symphyses may be mentioned also, as contributing to deaden and break the force of shocks passing through the pelvic arches; and these being generally, as we have seen, arranged in two layers allowing of limited sliding motion between them, are better calculated to resist *sudden shocks* passing *obliquely* than single discs, such as the vertebral, which are chiefly disposed to resist *pressure* passing *directly*.

The posterior projection of the iliac tuberosities protects the sacrum, deeply situated between them, from direct force tending to produce anterior dislocation, while their internal direction prevents that bone from slipping backward between them.

The great breadth and size of the sacrum in the human pelvis — it being proportionally *larger* than that of any other animal — indicate its importance as the basis of support to the spine, and the crown of the pelvic arch; and, in connection with the admirable mechanical and architectural arrangements just described, present a wide contrast to the pelvic structures of animals; and prove the erect position to have been designed for the habitual expression of the dignity of man.

The thigh of man, when standing, forms one line with the trunk, and makes an obtuse angle with the posterior arm of the pelvic lever; but in quadrupeds it is directed much more forwards, and forms an acute angle with both the ilia and the spine. In quadrupeds, the thighs are much closer together and more pressed upon the flanks, and, even when they rest on their haunches, they naturally support themselves on their fore legs. This is even seen to a great extent in the apes and monkeys, so difficult is it for them to maintain the centre of gravity in an erect posture. The extensors and flexors of the thigh on the pelvis are also more developed in man, in order to sustain with more firmness the erect posture. Hence the greater breadth of the hip and buttock, and the bulk of the thigh. The breadth of the pelvis also gives a greater leverage to these powerful muscles.

In walking, the human pelvis is thrown alternately, on each side, upwards, forwards, and sideways, as the leg on that side is lifted; the trunk keeping its centre of gravity over the bearing leg by swaying regularly to that side, the pelvic hoop being at the same time drawn over the supporting leg by the powerful abducting muscles, the glutei.

On account of the greater width of the pelvis and trochanters in the female, the centre of gravity oscillates through a greater space, and takes longer time to pass over from one leg to the other, and hence the greater amount of undulation in their gait, especially when running.

Mechanism of the human pelvis in regard to parturition. — As a containing cavity, when completed by its muscular and fascial structures, the pelvis offers a basin-shaped structure with a somewhat triangular superior aperture, the sides of which are formed by the psoæ muscles, and the base by the pubes; and with a moveable floor, formed by fasciæ and the levator ani muscle, and perforated by the rectum and generative organs. Its walls are interrupted laterally by the sacro-sciatic and obturator foramina, which are filled by soft and yielding muscular and ligamentous structures, and give way considerably to pressure from within, enlarging the pelvic diameters opposite to them. They afford, in common with the superior and inferior openings, the outlets for the nerves and vessels passing from the lumbar and sacral plexuses and iliac trunks to the inferior extremities and perineum. The inferior outlet also transmits the external communications of the pelvic viscera. These are, the bladder supported by the pubis; the rectum, supported by the sacrum and coccyx; and the internal organs of generation placed between them.

In the female these internal organs are more bulky than in the male, and consist of the uterus and its ovarian and vaginal appendages. That there is a relation between the greater size and the functions of these organs, and the greater extent of the female diameters, is evident from the consideration of their simultaneous development at the period of puberty, and corresponding increase afterwards.

This relative development of the pelvis seems to extend not only to *sex*, but to the *varieties* of mankind, either as an irrespective consequence of primitive formative type, or in regard to the adaptability of the fœtal head to the pelvis in the processes of parturition. In either case this adaptation is strikingly illustrated by the different pelvic forms prevailing in different races of men, which will be found, when considering that branch of our subject, to be markedly assimilated to the form of the skull.

The pelvic bone, which is of the greatest importance in an obstetric point of view, entering as it does into the formation of both the pelvic brim, cavity, and inferior outlet, is the *pubis*; and deformities of this bone produce the greatest obstacles to parturition. The sub-pubic arch is a peculiarity of the human species, it being only imperfectly developed in the lower animals; and it has an important bearing upon human parturition, in being compensatory for the great curve of the pelvic axis, and the change of direction forward of the inferior from the superior outlet. This curve is dependent upon, and follows the curve of, the sacro-coccygeal column, which, being more acute and directed more forwards below, affords the chief support in the earlier months of pregnancy to the uterus and its contents, which lie in the axis of the superior outlet, which axis, as we have seen, impinges below upon the coccygeal bone. Now, the coccyx, being principally held up in its forward position by the elastic sciatic ligaments and by the resilient ischio-coccygeus and levator ani muscles, affords a resisting support which is at once powerful and yielding, and acts like an elastic spring in supporting the uterus and its delicate contents under the effects of accidental shock. The female coccyx is much more mobile at every age than the male, and when ankylosed to the sacrum it is less favourable both to pregnancy and labour. In the more advanced stages of pregnancy, however, the uterus rises into the abdominal cavity, and rests mainly upon the smooth concave surfaces of the pubes and the soft muscular margins of the pelvic brim, being embraced and supported above and in front by the abdominal muscles. To allow the great expansion of the uterine contents, the broad ventral notch and expanding iliac wings are dispositions of great significance.

During labour, the fœtal head enters the brim of the pelvis in the oblique diameter, which being less encroached on by the muscles is the best adapted to receive it, as well as by its correspondence in form to the brim in that direction. Then traversing the pelvic axis, it passes, first downwards and backwards, and then, being turned forwards by the sacro-coccygeal curve, escapes under the pubic arch and through the inferior outlet. The fœtal occiput is directed generally in the left oblique diameter, towards the left ilio-pubic junction (in 69 per cent. of the cases — Naegele — to 80 per cent. — Boivin), and in its progress is twisted gradually forwards and towards the median line by the impingement of the parietal protuberance upon the inclined plane of the pyriformis muscle and upon the projecting ischial spine, until it emerges under the symphysis pubis, around which it turns vertically as round a centre; the real centre of its motion, however, being, as we have before seen, a little in front of and below the pubis. The more anterior part of the fœtal head, then, traversing the circumference of the sub-pubic circle, extends the coccyx, and passes between the tuber ischii, distending the sacro-sciatic ligaments and perineum, and turning, as it does so, on its own transverse axis.

In a well-formed woman, according to Naegele, the superior plane of the pelvis will be horizontal when the trunk is between the sitting and recumbent positions (*i. e.* when it forms an angle of 30° with the horizon). In such a position traction on the head of the child should be perpendicular.

In sustaining these evolutions, the pelvic circle necessarily is exposed to a force not hitherto considered, viz. pressure from within. In well-formed pelves this pressure will be exerted equally on all parts of the circumference, from the adaptation, before mentioned, of the child's head to the form of the pelvis. The strain, however, will be most evidently exerted upon the *ligaments* of the *pubic* and *sacro-iliac symphyses.*

The question whether these ligaments yielded during labour sufficiently to enlarge materially the diameters of the pelvis, is one which has attracted the attention of anatomists and obstetricians very much, particularly about the latter end of last century, when M. Sigault proposed, in lieu of the Cæsarian section, the section of the symphysis pubis, with a view of affording greater pelvic diameters.

Among the older writers on this subject Mauriceau, Peu, Lamotte, Vesalius, Varandens, Menard, and Voigt *denied* that separation of the pubic bones occurred during labour.

Some believed it to occur only in young primiparous females; others in primiparous females of advanced age; and others again only in pelvic distortions or peculiar circumstances of pregnancy.

Ambrose Parè, Pineus, Bauhineus Riveanus, Diemerbroek, Arniseus, Bianchi, Gregoire Pineau, Duvernay, Bertin, Levret, Santorini, Spigelius, and Smellie, have observed this separation in the *dead* parturient woman; and Guillemeau, Hildanus, Van Solingen, Veslingius, Puzos, Soumain, Bikker, Arnauld, and Morgagni in the *living* subject. Parè and Peu asserted that they had seen cases where the ilia had been separated from the sacrum; and Smellie relates a case where great pain at the sacro-iliac joints rendered this probable.

Of those who admit that relaxation of the ligaments and consequent separation do take place, Boivin, Louis, Severin, Pineau, and Meckel consider it to depend upon softening, thickening, and loosening of a *single* inter-pubic fibro-cartilage, and deposition of fluid in its meshes; Meckel with Antoine Petit, denying the frequent existence of a separation between *two* plates of cartilage. But Tenon found, that although, in most cases, the inter-pubic fibro-cartilage was single in the male, in woman it was generally double, and contained a slit or cavity, with no connecting fibrous tissue between the middle of the plates. And he found this to be the case in the young as well as the old, and before pregnancy as well as after; sometimes the slit was capillary, but in one female, recently delivered, the cavity would admit the forefinger. In none of his examinations did he find any thickening, softening, or laxity of the fibro-cartilage itself, however recent the accouchment, although the external investing ligaments of the joint were relaxed and elongated. He considers, that if in females where but one fibro-cartilaginous plate is present, separation of the bones occurs during labour, it must be by rupture of the fibres of the disc or its separation from the bone. It is, however, difficult to comprehend why elongation of these fibres should not take place as well as of those of the investing ligaments.

Tenon also asserts, that he has observed relaxation of the pubic ligaments, even in the male, during life. Sandifort considered that in women who have borne many children the pelvic ligaments become permanently looser. In a female aged 79, dissected by Cruveilhier, the symphysis pubis was exceedingly moveable, the sub-pubic ligament had disappeared, and a fibrous capsule invested the joint. Sœmmerring believes that separation of the pubes is not rare, even during easy labours, and that they remain permanently loose, and the pelvic diameters larger, after many labours. According to the last author, the sacro-iliac joints have also been found separated by a cavity of the width of an inch in females who have died during parturition. But it is a question, whether this was not caused by disease and deposit of pus. In a woman mentioned by Frank, in *Textors Neuem. Chiron.* (vol. i. p. 261.), the pelvis was so moveable every time she became pregnant, that she could not stand upright. Instances of separation of the pubic joint during labour are also mentioned by Eichelburg in *Rust's Magazine* (vol. xvii. part iii. p. 550.), and by Nicholson in *Trans. of Physic. in Ireland* (vol. iv. 1824). Dr. William Hunter, in his memoir upon this subject, gives two cases of parturient women, in which the fibrous tissue connecting the cartilages was replaced by a cavity lined by a perfect synovial membrane, and forming a perfect arthrodial joint; and he concludes, that a certain relaxation of the pelvic ligaments takes place in the latter months of pregnancy and during labour, allowing of a slight increase of the pelvic capacity, and a yielding to the shape of the fœtal skull.

On examining the pelves of five women who had died soon after delivery, Dr. Knox of Edinburgh found, in all, a remarkable relaxation of all the ligaments of the pelvic joints; in one the bones could be made to slide over each other. This anatomist also inclines to the opinion that this process is a regular and healthy one in the parturient female. This opinion is also supported by the post-mortem researches of the celebrated Rokitansky of Vienna, who considers that, in parturient women, the pelvic ligaments become soft, relaxed, and stretched.

In addition to the testimony on this side of the question, M. Senoir read an essay on the "*Articulations of the Female Pelvis*," at the Academy of Medicine of Paris, on the 1st of April, 1851; in which he concludes, 1st. That the articulations of the pelvis proper should not be considered as *amphiarthroses*, but as *arthroses;* and, 2ndly. That analogy of structure and composition leads him to think that an effusion of synovial fluid from the membrane lining the joints, causes the separation of the bones sometimes observed. (*Bulletin de l'Academie Nation. de Médecine*, t. xvi. No. 13. April 15th, 1851.)

It is, however, considered by Baudelocque, Boyer, Burns, Dewees, Denman, and I think most English writers on Obstetrics of the present day, that, in common cases, *no* sensible relaxation of the pelvic ligaments takes place, and that, when such relaxation does occur, it should be rather considered in the light of a morbid condition, as it adds very little to the diameters, and is attended with severe inconveniences from rupture of the sacro-iliac ligaments.

Notwithstanding, comparative anatomy, particularly in Cows, Seals and Guinea-pigs, to be presently considered, presents us with a strong analogical proof in favour of the doctrine of some parturient relaxation of the pelvic ligaments in women.

Comparative Anatomy of the Pelvis. — In the different races of mankind, the pelvis, as influencing in a very great degree the form of the body, presents considerable varieties.

Camper, and afterwards Sœmmerring, remarked that Negroes had more slender loins and hips than Europeans, consequent upon narrower pelves. Sœmmerring gives a comparative measurement of the diameters of the brim in a Negro and an European of adult size. In the *Negro*, he found 3 in. 11½ lines, long or transverse diameter; in the European, 4 in. 6 lines; in the Negro the short or conjugate diameter was 3 in. 7½ lines, and in the European, 3 in. 11 lines. From Camper's measurements, the long diameter was to the short one as 39 to 27½ in an adult Negro, and as 41 to 27 in an adult European, who, nevertheless, was of much less stature than the Negro.

The measurements in the table on page 151, were taken in the dissecting rooms of King's College, from an adult male Negro 6 feet high. From the measurement of this pelvis, the antero-posterior diameters seem to prevail in the Negro, and the whole pelvis to be smaller than in the European. This is seen remarkably in the limited breadth of the sacrum, (3 in. 9 lines), and in the approximation of the ischial spines (3 in.,) both much lower than the average European; the latter, indeed, less than in the Chimpanzee. In fact, I have never met with an European sacrum so narrow as in the Negro above mentioned, especially in an individual so tall as 6 feet.

This difference is remarkably contrasted in the pelvis of O'Byrne, the Irish giant, in the Hunterian Museum, in which the iliac wings are remarkably large in comparison with the true pelvis, and the sacrum very broad. The superior pelvic outlet is in this skeleton disproportionately larger than the inferior, the ischiadic tuberosities being nearly as close together as in ordinary-sized pelves. This sudden narrowing of the pelvis has evident reference to the better sustaining of the viscera of the pelvis and abdomen.

It is supposed that in Negro women generally, from the easy labours they undergo, there is much more proportionate pelvic capacity.*

The dimensions of the pelvis of a Negress of small stature, contained in Bonn's Museum at Amsterdam, are given by Dr. Hull in his *Second Letter to Simmonds*, as follows: At the *brim*, the conjugate diameter, $4\frac{3}{8}$ inches; the transverse, $4\frac{1}{8}$; the oblique, also $4\frac{1}{8}$ inches. From the inner extremity of the superior pubic ramus, to the sacro-iliac joint of the same side, $4\frac{1}{2}$ inches. At the *outlet*, the antero-posterior diameter (measuring from the apex of the sacrum) was, $4\frac{1}{8}$ inches; the transverse, $3\frac{1}{2}$ inches. The breadth of the sacrum was, $3\frac{1}{2}$ inches, and the length the same. The angle of the sub-pubic arch measured only $67\frac{1}{2}°$. In this pelvis also, although a female, the prevailing size of the antero-posterior diameters, and the limited breadth of the sacrum and transverse diameter of the outlet, as well as the exceedingly small expanse of the sub-pubic arch, are very remarkable, and are hardly accordant with easy labours, unless from the special adaptation of the fœtal head.

Dr. Vrolik of Amsterdam, who devoted much attention to this subject, remarks, that the Negro male pelvis is contrasted widely from the female of the same race, in being strong, dense, and massy, while that of the female is light and delicate in appearance, although not presenting the transparent thin parts that the pelvis of the European female exhibits. But the Negro male pelvis given in the table is remarkably light, slender, and well formed for a man of so considerable a stature, and the centres of the ilia very concave, and as thin as in most pelves I have seen; nor are the ischial tuberosities at all disproportionately large nor turned out, nor the posterior superior iliac spines elevated. Vrolik points out also, as marks of degradation in type in the Negro female pelvis, the vertical direction of the ilia, their elevation at the posterior superior spines, and the approximation of the anterior iliac spines to the cotyloid cavity, together with the narrow transverse and antero-posterior diameters, the anterior sacral projection, the general elongation of the pelvis, and the greater acuteness of the sub-pubic angle. This author considers these peculiarities to resemble the formation of the pelvis in the *Simiæ*. But as far as I have myself seen, there are very few characters indeed, either in the Negro or Bushman pelvis, which assimilate to those of the widely-different pelves of the Chimpanzee or Uran.

* This opinion is given by Mr. White, in his essay "*On the Gradation of the Human Species*," on the authority of surgeons employed in the Guinea trade; but I am informed by Mr. Edwards, a surgeon who has seen much of the West Indian creole negroes, that difficult labours are, on the contrary, *very frequent* among the females of these creoles, who are remarkable, like the males, for the thinness and narrowness of their flanks, and for the steady and easy walk which results from this formation. And he informs me also, that dystochia is not at all unfrequent even in the African negresses.

From the structure of the female *Bushman* pelvis, given by G. Cuvier, in Hist. Nat. des Mammifères, Dr. Vrolik draws the conclusion, that it presents greater animality of composition than even the Negro, as shown in the extreme vertical direction, narrowness, and height of the ilia, and the cylindrical form of the whole pelvis. The height of the ilia was much greater than in European females, while the width between the anterior iliac spines was less than even the smallest Negro pelvis. The spines of the ischia were, however, much wider apart, the sacrum more curved vertically, and the thinness of the iliac centres as little marked as in the Negro. The sacrum projected much forward at the base, and posteriorly was remarkable for the thickness and tuberosity of the lateral parts, and the posterior elevation of the coccygeal articulation, which were supposed to be for the purpose of affording attachment to the large gluteal masses of fat, characteristic of the Bushman race. The thickness, breadth, and posterior elevation of the ischial tuberosities, the posterior inclination of the cotyloid cavities, the prominence of the pubic symphysis, and the greater sub-pubic angle, were also remarked by Vrolik.

In the pelvis of a male Bushman recently added to the Hunterian Museum, I find the iliac wings to be short, broad, not much expanded, but considerably curved antero-posteriorly; with a crest arched, *ƒ*-shaped, and reaching as high as the middle of the fourth lumbar vertebra. The centres of the iliac wings are not thicker than is proportional, and there is a well-formed and deep internal concavity or venter. The pectineal eminence is well marked, but the ischial spines not so, and the ischial tuberosities are small and slender. The sacrum is short, much curved vertically, and elevated inferiorly, so as to project much behind, and diverging widely from the ischia, giving a wide and short appearance to the sacro-sciatic notch. The posterior lateral parts of the sacrum are *not* unusually thickened, but the sacral spinous processes are well marked and proportionally large, the two upper being very distinct, and separated from the crest. The shape of the brim is somewhat oblong and inclined to the Negro type, as may be seen from the measurements in the adjoining comparative table. The whole pelvis has a symmetrical, though a light, slender, and diminutive aspect corresponding to the diminutive stature of the individual. The breadth of the sacrum is even less than in the Negro, being exactly the same as the Uran-utan. The distance between the ischial spines is, however, greater, though that of the ischial tuberosities is less than in the Negro. The pelvi-vertebral angle in this skeleton seems to be less than usual, as far as one may venture to a conclusion from a dried skeleton. In a cast of a female Bojesman recently added to the King's College Museum, however, the vulva seems to be placed unusually far back, which may probably depend upon great obliquity of the pelvis.

The measurements of the *Tahitian* male pelvis, given in the table, corresponds, in the proximity of the ischial spines and narrowness of the sacrum, with the Negro and the Bushman, though its transverse diameters, unlike the Negro, are larger than the antero-posterior. In this respect, the Bushman more nearly approaches the Negro. The great antero-posterior diameter of the cavity shows a great vertical curvature of the sacrum. In the sacro-vertebral and pelvi-vertebral angles, the Bushman and Tahitian are nearly alike.

The pelvis of the female *Australian*, also in the Hunterian Museum, presents a very remarkable shallowness of the true pelvis. Otherwise, it is light and roomy, with well-expanded and very short ilia. The shape of the superior opening is of a perfect oval, with the transverse diameter half an inch larger than the antero-posterior. Though a much larger pelvis than that of the Bushman, its total depth is nearly as limited, and very much more so than in European female pelves of equal horizontal diameters.

In these specimens of races, considered by some to be more nearly related to the apes than the European, an examination of the adjoining table will show a very great pelvic difference between them and the highest apes, in the less proportionate preponderance of the antero-posterior over the transverse diameters, the shortness and expansion of the ilia, the less depth of the true pelvis both in front, sides, and behind, and especially in the more marked *sacro-vertebral angle*.

M. Vrolik describes the pelvis of the *Javanese* as very light in structure, of small size, and of a characteristic *circular* form at the superior opening, the bones being like those of a very young person, and the muscles correspondingly feeble. The small projection of the sacral promontory was also remarkable, as well as the great *inward* projection of the ischial spines, more marked, he says, than in the pelves of any other nation, and quite characteristic.

By the comparative measurement of many human pelves of different races, Professor Weber reduced them to four principal forms, distinguished by the general shape of the pelvic openings.

1st. *The oval form.*—The superior opening of an egg-shaped figure, narrow in front, broadest near the sacro-iliac symphysis, and again narrowing to the sacral promontory. The antero-posterior diameter smaller than the transverse. The ilia moderately distant, and obliquely placed; and the convergence of the walls of the true pelvis downward, also moderate. The sacrum moderate in breadth, length, and vertical curvature. The ischial tuberosities placed rather backward, and the spines widely distant. The subpubic angle neither very acute in the male, nor the arch very prominent in the female. Of this type, he makes two varieties, — viz. the oval or male-oval, and the round-oval or female-oval; the male variety of form being sometimes found in the female. Of this form he gives three specimens :—one of an European male; one, very large, of a Botocundo male; and one of the round or cross-oval form, in an European female pelvis, broad and shallow, with the transverse diameter 5 in., and the conjugate 3 in. 10 lines. The pelvis of the Australian female, given in the table, belongs to the round-oval form, and that of the male Tahitian to the male-oval form.

2nd. *The round form*, distinguished by the round or cross-formed superior opening, by the vertical sides, less anterior direction of pubes, and less projection of sacral promontory, making the conjugate of nearly the same extent as the transverse diameter. Of this form he gives five specimens, all females: — one European, two Negresses, one Hottentot, and one Javanese.

3rd. *The square or four-sided form*, distinguished by the great breadth of sacrum and horizontal flattening of pubes. The transverse diameter greater than the conjugate, but the superior opening forming nearly a square. Of this form are six specimens :— one of an European female ; two of Javanese male, and one of a female of the same race, and two Mestizos.

4th. *The cuneiform, or oblong form.* — Superior opening laterally compressed and oblong; sacrum very narrow; pubis with great anterior direction, so as to unite at an acute angle; with the conjugate greater than the transverse diameter. In the female, this form makes some approach to the oval shape. Of this form he gives eight specimens : — one of an European female, which has this shape very well marked, the conjugate diameter being 4 in. 9 lines ; one of a female Botocundo; one of a Negress ; one of a Negro ; one of a Kaffir ; and three others from Von Sœmmerring's collection. The pelves of the Bushman and Negro, given in the table, belong to this form.

M. Weber's conclusions drawn from these specimens are, that though the oval shape is most common in Europeans, the round shape in the American aborigines, the square shape in the Asiatic or Mongolian races, and the oblong in the Negro races; yet that none of the characters laid down by Vrolik are constant, nor belong exclusively to any particular race, but that deviations from the usual form in any race present characteristics which generally belong to other varieties of the human species.

The coincidence between the prevailing form of the skull and that of the pelvic brim in these classes of the human race is worthy of especial remark, and influences materially, as before mentioned, the adaptation of the fœtal skull to the pelvic passage during labour. After the form of the skull, that of the pelvis is perhaps the most characteristic of race of any in the body, because of its great influence upon the shape of the trunk ; and yet, from Weber's researches, it would appear that it is not sufficiently so to constitute a greater distinction than that of variety, and is not exclusive enough in its peculiarities to establish separate generic classifications of the human species.

In the *Simiæ*, and those even which most

Comparative Pelvic Dimensions.

Diameters.	Negro (Male). In. Lines.	Tahitian (Male). In. Lines.	Bushman (Male). In. Lines.	Australian (Female). In. Lines.	Adult Chimpanzee (Female). (Hunterian Museum.) In. Lines.	Chimpanzee. (K. C. Museum.) In. Lines.	Adult Uran-Utan. (Hunterian Museum.) In. Lines.	Gibbon variæ, (Female.) (Dr. Knox.) In. Lines
Of *brim* — Transverse	3 9	4 6	3 6	5 0	4 0	3 3	3 9	2 3
Oblique	4 3	4 3	3 8	5 0	5 3	4 9	4 9	
Antero-posterior	4 1	4 0	3 3	4 6	5 9	5 6	5 0	4 4½
Of *cavity* — Antero-posterior	4 9	4 9	3 10	4 9	5 0	3 0	4 0	
Of *inferior outlet* — Transverse (inter-sciatic)	3 3	4 0	3 2	4 6	3 9	4 0	2 9	3 0
Antero-posterior	3 0	3 3	3 5	4 0	4 6	3 6	4 0	
Between anterior superior iliac spines	8 6	8 6	7 3	8 3	10 0	5 6	11 0	4 0
Depth of true Pelvis.								
Between sacral promontory and tip of coccyx	- -	5 6	4 0	4 6	5 0	4 6	4 6	
Between ilio-pectineal eminence and sciatic tuberosity	4 3	3 9	3 6	2 10	4 10	3 6	4 0	
Between upper and lower border of symphysis pubis	1 9	1 6	1 3	1 3	2 6	1 10	2 0	
Depth of whole Pelvis.								
Between iliac crest and sciatic tuber	- -	8 0	7 0	7 6	10 9	9 0	9 6	5 4½
Between tuber ischii and *anterior* superior iliac spine	- -	6 6	5 6	6 0	9 6	8 0	8 0	
Between tuber ischii and *posterior* superior iliac spine	- -	6 3	5 6	6 0	10 0	9 0	8 6	
Between ischial spines	3 0	3 3	3 3	4 3	3 9	3 2	3 0	
Breadth of sacrum	3 9	3 9	3 3	4 6	3 0	2 3	3 3	
Angles — Sacro-vertebral	- -	120°	115°	135°	158°	145°	150°	
Pelvi-vertebral	- -	145°	145°	140°				
Sub-pubic	- -	60°	85°	90°	80°	60°	50°	

closely approach in osseous conformation the human race, as in the genera *Pithecus* and *Troglodytes*, the form of the pelvis is sufficient, at a glance, to distinguish them even from the Bushman and Australian, which have been seen to present all the pelvic peculiarities of the higher varieties of humanity.

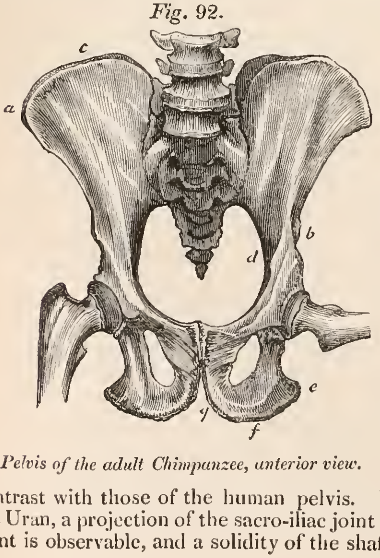
An inspection of the foregoing table will at once show this in the pelvic *diameters*. It will be seen that the antero-posterior diameters in the Chimpanzee, Uran-utan, and Gibbon prevail greatly over the transverse; that the *depth* both of the whole and the true pelvis is much greater than in the human pelvis; and that the sacrum is much narrower, especially in the Chimpanzee, and the ischial spines more closely approximated. The *sacro-vertebral angle*, too, is remarkably increased, especially in the Chimpanzee (160°), the sacrum being placed much more nearly in the direction of the whole spinal column, and having a less vertical, as well as a much less horizontal curvature, with no sacral promontory in the Chimpanzee, and little in the Uran; while the coccyx is straighter, and placed more in the line of the spinal column, and its tip is elevated above the level of the upper border of the symphysis pubis, so that the whole of the sacrum and coccyx is seen in front view. (*See fig.* 92.)

This high position of the coccyx is owing partly to the shortness of the *sacrum*, which is composed of three large flat vertebræ, all entering into the formation of the sacro-iliac joint, and united by ankylosis to two of the four coccygeal pieces in the Uran, and to one only in the Gibbons. In the Chimpanzee, however, there are four sacral vertebræ, *all* articulating laterally with the ilia, and the anterior sacral foramina are very small. The *coccyx* is composed of five vertebræ.

The *ilia* are much longer, thicker, more massive, and narrower, and present no central transparent portion nor internal fossa, being flat anteriorly and concave posteriorly, the reverse of the human ilia, and looking almost directly backwards and forwards, and very little inwards and upwards; so that, in these animals, there cannot be said to be any false pelvic cavity. In the Uran of the Hunterian Museum they are two thirds of the femurs in length, and measure 6 inches, and in the Chimpanzee 7 inches, reaching as high as the third lumbar vertebra. From the limited expansion of the wings, the anterior part seems deficient, the anterior superior spine (*a*) being placed directly over the cotyloid cavity; and the crest (*c*) being, consequently, very short, terminating abruptly at the vertical rib mentioned in the description of the human ilium. The *alæ* are more expanded in the Uran than the Chimpanzee. The crest does not present the lateral *f*-like curvature, and is less arched than in man. The anterior iliac spines are more widely separated, the inferior (*b*) being scarcely discernible, and the border between them thin and concave. The posterior, or iliac tuberosity is even less prominent in these animals than in the lower order of Ruminants. The distance from the cotyloid to the sacro-iliac joint is 3¼ inches in the Hunterian Chimpanzee, and about 3 inches in the Uran, though, from the greater straightness and obliquity of the cotylo-sacral arch (*d*) and the want of the anterior curve, the *direct* horizontal distance between these points is about the same as in man.

In the *Simiæ* generally, the ilia are said to be placed almost in a straight line with the spinal column. Added to the great length of the ilia, this arrangement causes the pelvic brim to be much elongated from before backwards; but much less so, however, than it would be if the pubes and iliac shafts were in the same plane. I have, however, found the *ilio-vertebral angle* in Chimpanzee, Uran, long-armed Gibbon, and brown Baboon to be very little, if at all greater than the human *pelvi-vertebral*, as far as could be ascertained without actual section of the bones. But in the Lemurs the ilia are only 10° from being in the same straight line with the spine; while in the Mandrill and many Monkeys they are almost parallel. This characteristic, heightened by that of the much diminished curve of the lumbar vertebra and the elongation of the iliac shafts in these animals, contributes to form a great

Fig. 92.



Pelvis of the adult Chimpanzee, anterior view.

contrast with those of the human pelvis. In the Uran, a projection of the sacro-iliac joint in front is observable, and a solidity of the shafts of the ilia. Blainville remarks, that the sacro-iliac facet is oval in these animals.

The *ischia*, in common with the whole pelvis, are longer in the Chimpanzee than in the Uran; and the ischial tuberosities (*e*) more turned outwards. In both, however, they are directed much more in the line of the ilia than in the human species, the *ilio-ischial angle* being 165°; and are larger, more flattened, spread, and diverging. The ischial spines in these animals begin to degenerate, and are rather rounded eminences or ridges than true spines; and the inferior rami (*f*) are directed almost horizontally inwards, leaving a large triangular foramen obturatorium, and entering into the formation of the pubic symphysis (*g*), which in the *Simiæ* generally, may be more properly called the *ischio-pubic* symphysis. The whole of the ischial portion of the pelvis has a more anterior position, and a more laterally flattened appearance than in the human pelvis. The cotyloid cavities are small, elongated vertically, and deeper behind than above. The sciatic notches are long and narrow.

One of the most remarkable differences from the human pelvis, however, is the *difference of direction* of the *ilia* and *pubes* with regard to the transverse-vertical plane of the spinal column, an arrangement which bends the plane of the pelvic brim at the ilio-pectineal eminence in different directions. In the Chimpanzee, the antero-posterior *angle*, formed by the superior ramus of the pubis with the cotylo-sacral arch of the ilium, is 120°, and in the Uran 125°; constituting a striking difference from the human pelvis, where the cotylo-sacral and pubic arches are in one plane.

This alteration in the direction of the pubis will be found to be a great characteristic of all quadrupeds, in the prone position of whose bodies the pubis has a tendency to be placed more vertical and more anterior, to be out of the way of the femurs in their angular movements. In the Sloths and Anteaters, the pubis will be seen to be turned in the *opposite direction*, yet still forming an *angle* with the ilium, but with the retiring sides turned backwards. I think, therefore, we may safely take the *ilio-pubic angle* as a general peculiarity of the inferior animals possessing pelves, and one which distinguishes them, as far as I have seen, *universally*, from the human species (see *page* 173. *fig*. 112. 2 —13.).

A remarkable consequence of this more horizontal direction of the pubis in the *Simiæ* is the disappearance of the *angle of the symphysis*, it being quite parallel with the spinal column. And this parallel position is, according to Cuvier, a mark of distinction between all the brute creation and man. In other respects, the pubis of the *Simiæ* is short, little arched, and without marked spine. The inferior outlet of the pelvis is larger than it would otherwise be, from the elevation of the coccyx, and, from the shortness of the sacrum, and length of the ischio-pubic symphysis, its plane is more parallel, and its axis more in a line with those of the brim than in man.

So we see, in these animals, a marked and evident degeneracy of pelvic structure, allying them much more closely to the quadrupeds, especially to the *Carnivora*, than to mankind. And we may remark, more especially, that their fitness for the habitual *erect* position is much diminished by the want of *direct* antero-posterior extension of the pelvis, produced by the flatness of the sacrum and the less marked sacro-vertebral angle, and the shortness and change of direction of the pubis; which renders the arms of the pelvic lever shorter from the cotyloid fulcrum, and the hold of the extensor and flexor muscles of the thigh less powerful in maintaining the standing posture. And, corresponding to this, we see in these animals. great diminution in the bulk of these muscles, particularly in the *glutei* and *gastrocnemii*, the plumpness of which constitute the buttocks and calves characteristic of the human figure From this cause, the gait of these animals in bipedal progression is very unsteady.

The expanded, everted, and large ischial tuberosities, and the strength of the ischio-sacral arch, indicate that the *sitting* posture is more natural to the Simial race; while the greater depth of the posterior than the superior part of the cotyloid brim shows, as well as the marked ilio-pubic angle, a provision for femoral support in a semiflexed, rather than an extended position. In the erect posture, from the flatness of the pelvis, the ischial tuberosities are brought close upon the femurs, and reach nearly half-way down their short shafts, interfering much with their motion.

According to Grant and Wagner, there is no cotyloid notch nor ligamentum teres in the Orangs; but the cotyloid notch is present, though small, in the skeletons I have examined.

In the *Hylobatis Lar*, or long-armed Gibbon, the *iliac* wings are flatter, and directed still more antero-posteriorly, crest rounded, large, and elevated; *ischia* short, in a right line with the ilia, with flattened and expanded tuberosities, spines more distinctly marked, and rami directed, like the elongated *pubes*, more directly inwards. The cotyloid cavities are thus more widely separated, and the superior pelvic outlet has a triangular form, with the small end directed backwards. The *sacrum* is narrow and flat, forming a large angle with the spine, and composed of five vertebræ, of which the three upper, considered by Blainville to be the only true sacral vertebræ, articulate with the ilia. The *coccyx*, consisting, according to Blainville, of seven, according to others, of five vertebræ, is short, there being no tail. The inferior outlet is large, and the true pelvis shallow, from the shortness and expansion of ischia.

The subgenera *Callithrix*, *Cercocebus*, and *Semnopithecus* present an elongation of the *coccyx* into a caudal appendage with prehensile attributes, and perforated for the continuation of the spinal cord, which widens still more the progressive separation from the human type. In the Squirrel Monkey are three *sacral* bones, of which the two upper articulate with the *ilia*, and the broad transverse processes of the last project towards the *ischia*, so as to give a square outline to the inferior outlet. Ischial tuberosities not flattened. In the Capuchin Monkey the *ilia* are parallel with the spine, the *ischia* are inclined forwards to the abdominal surface, and the *pubes* are more oblique. In the *Semnopithecus entellus* the *sacrum* is more arched laterally and broader. The *ilia* are prismatic and long, and project more behind the spinal column. The *ischia* and *pubes* are short, with flattened and expanded tuberosities, and no ischial spine. Ilio-pectineal eminence marked. In these tribes the posterior border of the elongated ilia is the thickest part of the bone, the anterior part being thinned and spread out more or less. The *pubes* are generally placed nearly at *right angles* to the ilia, and the *lumbo-iliac angle* is about 160°.

Of the genus *Cercopithecus*, or Baboon tribe, there is, in the brown Baboon, a well marked *sacro-vertebral angle* (155°); the two upper of the three *sacral* vertebræ only articulate with the ilia. The *caudal* vertebræ are not numerous. The *ilia* are more expanded, but still present the posterior concavity. The *ischia* are short, with very broad and flattened tuberosities. The *pubes* are flattened, with an acute superior border, and rostrated at the symphysis. *Ilio-pubic angle* more marked (110°). In the Mandrill, *Papio Marmon*, the *sacrum* is more arched both vertically and transversely, and the promontory better marked. The *coccygeal* vertebræ are four in number, and there is no tail. The *ilia* are parallel with the spine, directly under which are placed the cotyloid cavities. The *ischia* are short, with much-expanded and flat tubers. The *pubes* are at right angles, both to ilia and spine, and the ischio-pubic symphysis is very little advanced before the plane of the spinal column.

In the *Sapajous*, or American Monkeys, there are three *sacral* vertebræ, of which the first only articulates with the ilia in the *Onistiti*. In the White-bellied *Ateles* the *ilia* are longer and more expanded; *pubes* more oblique; *ischia* short, with no spine, and small tuberosities. In the *Saimiri* there is a very short ilio-ischium.

In the *Lemurs*, or Makis, the *sacrum* is in a right line with the spine. Of the three sacral vertebræ, the first only articulates with the ilia, and the last is not ossified to the second. They differ little from the lumbar vertebræ, except in the thicker transverse processes. *Caudal* vertebræ numerous. The pelvis generally is very weak, narrow, and short. The *ilia* are narrow and almost parallel with the spine, and the ilio-pectineal eminence is unusually well marked; but the *ischial* tuberosities are delicate, indicating the less frequent sitting posture in these animals, and a still greater tendency to quadruped progression. In the *Lemur albifrons*, however, the *sacrum* is broader; *ilia* more expanded; *ischial* tuberosities larger and more expanded; *ilio-pubic angle* 120°. In *L. tardigradus* the *sacrum* is long, narrow, and keeled in the middle, being ankylosed to the last lumbar and three first *coccygeal* vertebræ, as in birds.

The *ilia* are narrow and cylindrical; *pubes* long, large, oblique, with no ilio-pectineal apophysis; *ischia* short, with horizontal rami and tuberosities passing backward to articulate with the transverse processes of the upper coccygeal vertebræ, another bird-like arrangement. In *L. indri* the *sacral* pieces are four, with complete ankylosis, the two or three upper articulating with the ilia. *Ilia* expanded, with extended crest and external fossa, and reaching to the penultimate lumbar vertebræ; *ischia* very short, with more expanded tubers; *pubes* less oblique. In *L. volans*, or *Galeopithecus*, the *sacrum* has five vertebræ, the first only articulating with ilia. *Ilia* small and narrow; *ischia* with large posterior angle; *pubic symphysis* very short. In the subgenus *Sterops*, the slender Loris presents a remarkably elongated and contracted pelvis. The *sacrum* is long and narrow, with the two upper pieces articulating with ilia. *Ilia* slender, long and columnar, and nearly parallel with spinal column; *ischia* small, flattened laterally, placed in a line with the ilia, and very near each other, so that the cotyloid cavities are closely approximated; the lateral diameters very short, and the inferior outlet a mere chink. The *pubes* are long, projecting forwards, downwards, and inwards, being inclined to each other at an angle of 40°, causing the superior outlet to be triangular, with the base at the *inter-cotyloid diameter*, and the apex at the symphysis pubis. This pelvis is also remarkable for the extreme angularity of the pubic portion with the iliac, the *ilio-pubic angle* being 75°, or less than a right angle, the only instance of the kind I have met with. (*See fig.* 93. *a*, *b*, *c*.).

Fig. 93.

Pelvis of the slender Loris, lateral view.

The animals most allied to the preceding order of primates in the form of the pelvis, taken in conjunction with their general structure, are the *Carnivora*. In these, as in most multidigital animals, the pelvis is so contracted that the trunk resembles an inverted pyramid; whereas in man, constructed for an erect posture, the base of the pyramid is in the pelvis. Climbing animals, such as the Apes, Bears, and Sloths, present the nearest approach to the human structure in this particular.

In estimating the *sacro-* and *ilio-vertebral angles* in the succeeding orders of Mammalia, it should be observed that, from the coincidence of the lumbar curve with the great dorsal curvature of the spinal column and the elevation of the neck, the vertebræ cannot be considered as being placed in one general plane, as in man. The line of direction of the lumbar vertebræ has, therefore, been taken for the sacral and iliac angles.

The *sacrum*, in the *Carnivora* (*a*, *fig.* 94.), is narrow, flat, and triangular, with long and distinct spinous processes, and placed almost in a right line with the spine. In the Bear, however, from its climbing habits, the sacrum is broader, larger, and more massy, and the sacro-vertebral angle more marked. The number of sacral vertebræ is three in the great majority of the species, the two upper articulating with the ilia; but in the Hyæna there are but two, in the Tiger four, in the brown Bear five, and in the white Bear as many as seven. The *coccygeal* or caudal vertebræ (*b*) are generally very numerous.

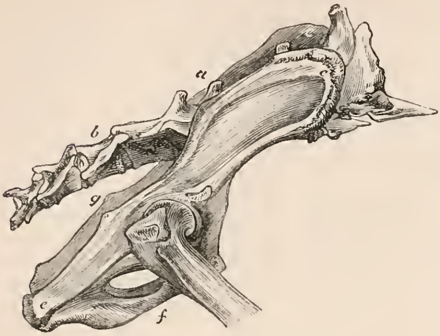
The *ilia* are moderately long, thick, and narrow in their whole extent, and are placed very obliquely upon the lumbar vertebræ, forming with them an angle of about 150° to 160°; but in the Bear and Hyæna 140° only. The external surface of the elongated iliac wing is concave, and the internal flat and turned inwards towards the spine; the crest (*c*) thick, narrow, acutely arched, and projecting backwards beyond the spinal column. The *ischia* are long, strong, prismatic, somewhat expanded posteriorly, and considerably divergent, but directed *in the same antero-posterior plane* with the ilia, forming together a very long ilio-ischion element. This disappearance of the antero-posterior, ilio-ischial angle, which commenced in the Apes, is, in the *Carnivora*, arrived at its greatest extent, and in the Tiger is even *reversed* or bent downwards in the opposite direction about 15° (see *fig.* 112. 5). With the great obliquity of the ilia, this affords, in the quadruped position, a longer and more powerful leverage for the muscles of the hinder extremities to execute their characteristic bounds, and, like the reverse formation of the ilio-pubic angle, it is another great distinction between these and human pelves. The ischial tuberosities (*e*) have an outward direction, as well as the ischia generally, and the spine (*g*) is a mere rudimentary ridge. The *pubes* are short, and the symphysis (*f*) is long, being formed generally both by the ischium and pubis. The *ilio-pubic angle* varies from 110° in the Tiger, to 120° in the Lion and Leopard, and 125° in the Bear and Hyæna.

The anterior pelvic outlet is smaller than the posterior, from the divergence of the ischia posteriorly; and the cotyloid cavities are inclined outwards slightly, so as to overhang the femora in the prone position.

The centre of gravity, in these animals, being placed much nearer the anterior than the posterior extremities, the former bear the most of the weight, while the latter act more as impelling agents in the powerful bounds which they execute.

The *ilia* of the Bear are shorter, thicker, and more massive, with more expanded wings, a better-marked anterior superior spine, and a more marked lumbo-iliac angle; the *ischia* short and widely expanded, and the *pubes* remarkably strong, with a very long symphysis. At the anterior pelvic outlet, the transverse diameter is a little larger than the antero-pos-

Fig. 94.



Pelvis of the Lion, side view.

terior, and the acetabula are large and deep. In the Badger the *ilia* and *ischia* are large, expanded, and curved outwards at their free extremities. The iliac shaft is prismatic, with an *ilio-lumbar angle* of 140°. The *pubes* are rather long, with an elongated symphysis, and form an angle with the ilia of about 130°. The same general conformation is evident in the Racoons and Coatis, the *ilio-ischial angle* being, however, somewhat better marked, and the *ilio-pubic* about 145°. The Coatis have but one sacral vertebra. In the Hyæna, also, the *iliac* wings are considerably spread, with a very pointed anterior spine. In the Dingo the *ischio-pubic* element is very short, the anterior outlet and obturator foramina small, but the posterior outlet larger. The Weasel has a very small pelvis, with but two sacral vertebræ, one only articulating with upper extremities of the long iliac shafts.

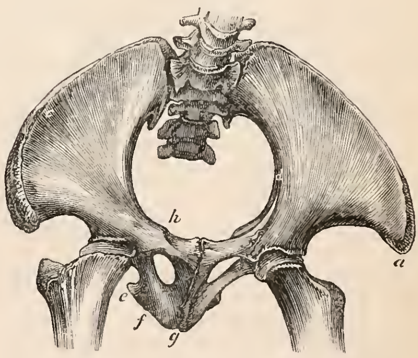
In the *Phocæ* the *sacrum* has four vertebræ, the first only articulating with ilia, and much wider in its transverse processes than the rest; the *ilia* are extremely short, thick, and curved outwards, with very small external fossæ; the *ischia* are long and slender, with small tuberosities almost touching the second coccygeal vertebra, with long rami not forming a symphysis, but directed backward to meet the pubis. The *pubes* are very long, slender, and oblique, with a short symphysis, and including a very large, oval obturator foramen. The pelvis altogether somewhat resembles that of the Badger, with the superior opening much elongated antero-posteriorly, and triangular in shape, with the base at the sacrum. The shortness of the ilia alone indicates the great contraction of the posterior extremities for their swimming requirements. Dr. Knox has observed, in a pregnant female Seal, a separation of the symphysis pubis, and elongation of its ligaments to the extent of nearly 2 inches, such as Le Gallois has described in the Guinea-pig. He found, moreover, that such a separation of the bones produced much more enlargement of diameters in these elongated triangular pelves than in the transverse oval form of the human female.

In the order of pelvic development, the *Pachydermata* occupy a very high place, being characterised by great massiveness, proportionate shallowness, and perpendicularity of pelvis, and large and overhanging acetabula, the better to support the immense weight of these animals, thrown more on the hinder extremities than in the *Carnivora*, from their bulky dorsal structures and abdominal viscera. The ischial spinous ridges and anterior inferior iliac spines are faintly marked or wanting, the sacral spines are coalesced into a continuous crest, and there is little or no sacral promontory.

The *sacrum* of the Elephant (*fig.* 95.) is comparatively very narrow, flat, and short, and placed on the spine at an angle almost imperceptible; the number of vertebræ being four only, according to Cuvier. The *coccygeal* vertebræ are numerous.

The *ilia* are short, broad, massy, fan-shaped, and much expanded, with a large concavity or iliac fossa directed forwards and downwards, the dorsum being alternately concave and convex. The iliac crest (*c*) is large and flat-arched, with the anterior superior spine (*a*) hooked suddenly downwards, and the posterior inferior directed backward from the sacro-iliac joint, to afford leverage to the powerful sacro-iliac ligament. There are no well-marked iliac ribs, except the cotylo-sacral (*d*), which is very strong and massy. The *ischia* are moderately short, and form an *ilio-ischial angle* about 145°, presenting no spine, and having the tuberosities (*e*) directed

Fig. 95.



Pelvis of the Elephant, front view.

dorsally, and the rami (*f*) vertically towards the abdominal surface. The *pubes* are short, and directed almost horizontally inwards, with a well-marked ilio-pectineal spine (*h*). The symphysis (*g*) is parallel to the vertebræ, and very long, including the whole of the short ischial rami as far as the rough portion forming the tuberosity, so that the ischio-pubic symphysis extends as far backwards as the tuberosities. The sciatic notches are wide and open, but the obturator foramina are smaller than the cotyloid fossæ, which are very large and overhang much at the superior or dorsal part. The planes of the acetabula are inclined from the perpendicular about 70° in the elephant, being about 5° more than in the fossil Megatherium and Mylodon. The pelvis of the Elephant is altogether remarkable for its perpendicular position, the *lumbo-iliac angle* being about 120° only, and the pubes being advanced as far forward as the iliac crest, at an angle of 100° with the ilia. Thus the posterior limbs are brought more under the weight of the animal. The superior outlet is roundish, but broader at the pubes than at the sacrum, and the antero-posterior diameter is but little larger than the transverse. In the fossil Elephant, however, the antero-posterior diameter is greater in proportion. The female Elephant has the pelvis more open than the male, and the borders more trenchant, according to Cuvier. Blumenbach states that the round ligament, as well as the cotyloid depression, is wanting in the Elephant.

The pelvis of the fossil Mastodon is much less depressed and expanded than that of the Elephant, according to Cuvier, and its outlets smaller, showing that its abdomen was of less size.

The Rhinoceros has four *sacral* vertebræ, three articulating with the ilia, and supported by articulation with last lumbar transverse processes; and the *caudal* vertebræ numerous.

The *ilia* are large, massy, short, and expanded, though much less so than in the Elephant; with the anterior iliac fossa well marked, and the dorsum also generally concave from side to side, from the backward curvature of the inner border to be applied to the sacrum. The crest is large, and the anterior superior spine turned forwards, as in the Elephant, and forked at the end. The *ischia* are longer than in the Elephant, with thick tuberosities, turned much outwards. *Pubes* long, and united at a sharper angle, with prominent ischio-pubic symphysis. The *lumbo-iliac angle* in the two-horned variety is 125°, the *ilio-ischial* 145°, and the *ilio-pubic* 150°, making the pubis nearly at right angles to the spine. The whole pelvis is shallow, with the ischio-pubic portion placed more backward than in the Elephant. The anterior outlet is large and oval, with the longer diameter antero-posterior. In the fossil variety there is no fork on the anterior superior iliac spine, and the obturator foramina are more elongated.

In the Hippopotamus the *sacrum* is very broad and flat from side to side, though arched considerably longitudinally; with a considerable angle, and articulated with last lumbar transverse processes. The *iliac* wings are almost plane with it, forming a *lumbo-iliac angle* of about 150°, and are less expanded, smaller, and more slightly convex, with the two superior spines directed much dorsally, especially the posterior. The *ischia* are long and comparatively slender, and directed dorsally, forming a large angle with the ilia, and supporting large and massy tuberosities, which are parallel to each other, and project by a prominent tubercle dorsally above the coccygeal vertebræ, a peculiarity which causes this pelvis to look altogether like that of the Ox. The *pubes* are elongated, and the ischio-pubic symphysis also long. The obturator foramen is large, and the plane of the acetabulum looks downwards and outwards, and is placed at an angle of about 50° from the perpendicular, being 20° less than that of the Elephant. The whole pelvis has an open, light, oblique, and flat appearance, with the ischio-pubic portion placed more backwards than either the Elephant or Rhinoceros.

In the Hog the *sacrum* is narrow, the *ilia* and *ischia* more elongated, and the latter closer to each other, with prominent and parallel tuberosities. The whole pelvis is elongated and approaches the *Carnivora* type, as is particularly seen in the *ilio-pubic angle* (120°). The *lumbo-iliac* angle is about 145°.

In the Tapir are three sacral vertebræ, the two upper articulating with ilia, and forming a *sacrum* arched considerably, both transversely and longitudinally, and with an imperceptible angle. The *ilia* are remarkable for their long and somewhat rounded shafts, and the sudden expansion of the wings on each side, so as to form a T shape, of which the branches are directed obliquely antero-posteriorly, the posterior branch being articulated to the sacrum, into which they bite well. The crest is thus made slightly *concave* instead of *convex*. The sacro-iliac facet, which in most mammalia is lunated in shape, with the convexity directed to the acetabulum, and the concavity to the spinal column, is in the Tapir of a peculiar shape, narrowing suddenly between the two sacral vertebra, and then again expanding, forming two distinct sacral "joggles." The *ischia* are long, with tubers projecting dorsally; *pubes* directed inwards. The *lumbo-iliac angle* is comparatively very acute (125°); the *ilio-pubic* large (145°); and the *ilio-ischial* well pronounced (140°). The whole pelvis is very like that of the Horse, but is distinguished by the greater breadth and curves of sacrum, and by more massy proportions, and more distinct T-shaped, and greater expansion of the ilia. The pelvis of the fossil *Paleotherium* has some resemblance to that of the Tapir, but the *ilia* are longer and more prismatic, and the *ischial* tuberosities less developed. That of the *Anoplotherium* is a link between the Tapir and Camel.

The *Solidungula* form a connecting pelvic link between the foregoing and the Ruminants.

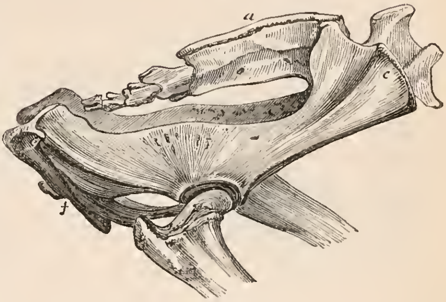
The *sacrum* of the Horse is flat, not curved longitudinally so much as in Ruminants, and placed in the line of the dorsal curve. It is moderately broad between the ilia, but narrows suddenly posteriorly, and reaches as far backwards as the middle of the ischia. This is the same position as in the Pachyderms proper; but in the Ruminants, whose pelves are more oblique, the sacrum scarcely reaches to the symphysis pubis, as is seen in the pelvis of the Ox (*fig.* 97.). The sacral pieces are six in number, two only articulating with the ilia, and the sacral spines are *not* united in a crest. The *ilia* approach in shape to those of the Tapir, being in a less marked degree T-shaped; the posterior limb of the iliac wings projecting inwards as far as the sacral spines; the anterior superior spine often presenting an epiphysis, and the shaft being long and blade-like. The *ischia* are comparatively long, and much more slender than in the Ruminants, being placed nearly parallel with the coccygeal vertebra, and with prolonged tuberosities. The *pubes* are small and short, and directed a little forwards, as well as downward and inward, with a marked ilio-pectineal eminence, and a very long ischio-pubic symphysis. The sciatic notch is wide, and the obturator foramen small. The anterior outlet is large and squarish, and the posterior elongated vertically and somewhat diamond shaped. *Lumbo-iliac angle* rather larger than that of the Tapir, being about 130°; *ilio-ischial*, 145°; and the *ilio-pubic* about 130°; making the *lumbo-pubic* rather less than a right angle.

In the *Ruminantia* the *sacrum* is composed generally of four vertebræ, the two upper articulating with the ilia. In the Gazelle and Antelope, however, there are five, and in the common Stag only three. The sacrum is proportionably broad, and more arched, both longitudinally and laterally, than in the preceding orders. The sacral promontory is also better marked, and the *sacro-lumbar angle* more perceptible. In the Ox, especially, this reaches to about 145° to 150°, and in the Fallow-deer 160°. The sacral spines are coalesced in a perfect crest in the Ox, Fallow-deer, and Stag (*fig.* 96. *a*), and partially in the gigantic Irish deer, Gnu, and Equine antelope; not so in the Giraffe and Camel. The *caudal* vertebræ are numerous.

The *ilia* are long, with the crest (*c*) concave, and the alæ expanding laterally at the top, especially in the heavier Ruminants; being concave internally, and convex externally, and projecting much over the dorsal surface of the spinal column, by the flattened and elongated posterior superior spine (*b*). They form little of the abdominal parietes, and are placed on the spine at an angle of 140° to 150°. The *ischia* are long and large, and placed on the ilia at an angle (*c d e*) of about 150° in the Deer and Sheep tribes, but much less in the heavier animals. This increased length and size of the ischia is particularly marked in the Deer tribe; and, as fulfilling the same mechanical requirements for affording a long and strong hold for the powerful extensor group of pelvic muscles, allies them with the Carnivora, and other *springing* animals afterwards to be considered.

The large and flattened tuberosities (*e*) project much on the dorsal surface of the pelvis. This is especially seen in the Fallow-deer, common Stag, and Ox, with a well-marked lateral tubercle (*g*), which is also present in the Gazelle and Roebuck. They present no ischial spine, except in the Lama, where it is well marked. The *pubes* are very short and slender, and are directed from without almost directly inwards, forming an *ilio-pubic angle* of about 130° to 140°. The

Fig. 96.



Pelvis of the Stag, lateral view.

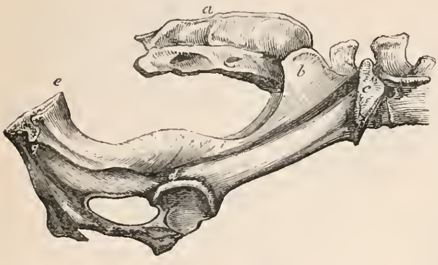
ilio-pectineal spine is much marked in Red deer. Generally the ischia form part of the elongated symphysis (*f*).

In the Ox, the *symphysis* is not placed quite parallel to the spine, as is usually the case in the inferior animals; but is placed *obliquely*, as in the human species, diverging more from the spine at the anterior than at the posterior extremity, and forming with it an angle of about 20°, and causing the anterior opening to be larger than the posterior (see *fig.* 97. *f*). The anterior opening is large and roundish, with a prevalence of the antero-posterior diameter. The posterior opening is more square, but irregular and looking much upwards.

The ischio-pubic portion of the pelvis is altogether very long, and opposed to the coccygeal vertebræ. In Deer, Goats, and Ruminants generally, but especially in the Ox, the gradual upward curve of the ischia, and the well-marked dorsal projection of their tuberosities, cause them to appear prominently on the rump, projecting on each side and above the coccygeal vertebræ (*figs.* 96, and 97. *e*.) In the Ox the *ilio-ischial angle* is as much as 130°; and the *lumbo-iliac angle* being about 150°, the acetabula are thereby placed directly under the last bone of the sacrum, and at the apex of an inverted arch (*c d e*) formed by the ischium and ilium. By this elevation of the ischia, the sacro-sciatic ligaments become a means of support to the sacrum, as well as the sacro-iliac, and thus that bone becomes suspended between two curved springs, formed by the ilio-ischion on each side.

Thus in these animals the sacro-sciatic ligaments resist motion of the sacrum in a direction downwards and forwards, a direction totally contrary to those of the human pelvis, as considered in the section relating to the mechanism of that structure. And this change of function, so simply transitionary, results from the alteration of mechanical requirements in the quadrupedal position of the trunk. About the period of parturition, the sacrum of the Ox is said to sink evidently between the ilia and ischial tuberosities, by relaxation of these ligaments. The elevation of the ischial tuberosities doubtless would make such a change of position more evident in the Ox than in other domestic animals.

Fig. 97.



Pelvis of the Ox, showing the ilio-ischial angle (*c d e*).

It is somewhat interesting, that, in most animals with flat sacral bones, the axes of the anterior and posterior pelvic openings, as well as that of the tubular cavity, coincide in the same straight line. In the Cow, however, and in some other Ruminants, these axes form a considerable angle one with the other, on account of the greater curve of the sacrum. This will, doubtless, have considerable influence in producing the more laborious parturition of these animals, which usually requires artificial assistance.

In the Ox the planes of the acetabula are inclined about 40° from the perpendicular. The pelvis of the gigantic Irish deer also presents markedly this arrangement.

In the American elk, the pelvis is rather elongated and narrow, being small and weak in comparison with the rest of the skeleton. There is the dorsal projection of ischial tuberosities; and the ischio-pubic symphysis is long, and diverges slightly from the spine *posteriorly*.

In the Camel the sacro-vertebral angle is well marked; the sacrum is much curved, and composed of four pieces. The *ilia* are long, strong, and blade-like, with the anterior spine prolonged downwards and the alæ convex anteriorly. The *ischia* are comparatively very short and feeble, set at a larger angle on the ilia, and present a feebly marked spinal ridge, and a well-marked outward projection at the tuberosities. The *pubes* are broad and moderately long, with a better marked *ilio-pubic angle* (120°) than in the preceding, and the ischio-pubic symphysis is long and divergent anteriorly from the spine, as in the Ox, the centre being opposite the last sacral bone. The foramen obturatorium is small, and the anterior outlet large and oval. The *lumbo-iliac* angle is about 140°, and the lumbo-pubic is rather less than a right angle.

In the Giraffe the *sacrum* is narrow, and its angle with the spine indistinct. The *ilia* are not very long, and the crest, unlike most Ruminants, is convex instead of concave, the wings being expanded and concave internally. The *ischia* are long and curved upwards, with everted and laterally flattened tuberosities. The *pubes* short and very thick, with long symphysis, forming a thick tuberosity, and much diverging from spinal column anteriorly. *Ilio-pubic angle* large, 140°; *lumbo-iliac*, 150°.

In Sheep and Goats the *sacrum* is broad, and its angle indistinct. The *ilia* are long and blade-like, with scanty wings; *lumbo-iliac angle*, 145°. *Ischia* broad and short, with large laterally projecting tuberosities; and a rudimentary spine in the Ram. The *pubes* are longer than in Deer, and directed horizontally inwards. The pelvic outlets are large, as also are the sacro-vertebral and ilio-ischial angles.

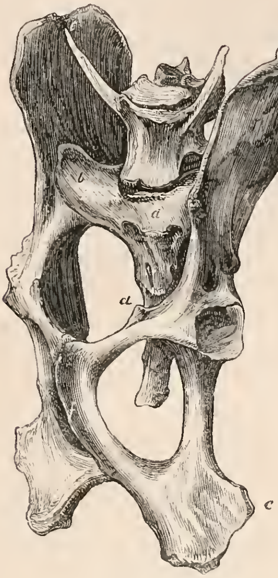
A very distinctive pelvic peculiarity is seen in the *Meminna*, or Pigmy Chevrotain. The *ilia* and *ischia* are, in this curious animal, *ankylosed* to the *sacral* vertebræ. The osseous ridges in the site of the oblique posterior ilio-sacral ligaments are very prominent, and the ossified sacro-sciatic ligaments are distinct and well marked. The sciatic notch is thus converted into a foramen, and the pelvis resembles in this respect that of the Sloth. In the Musk Deer, also, the last sacral transverse processes nearly abut on the short and dorsally projecting ischia. In the heavier Ruminants, as the Camel, gigantic Deer, and Ox, the pelvis has somewhat of the heavy appearance and overhanging acetabula of the Pachyderms, but in the lighter Deer and Goats it becomes gradually more slender and elegant in form, and more oblique in direction.

In the *Rodentia*, the pelvis is largely developed for the support of the powerful hinder extremities in leaping, the most usual mode of progression of the generality of these animals.

The *sacrum* is generally continued in a line with the lumbar curve in the long-tailed species. In Hares and Rabbits, however, the sacrum is considerably arched, longitudinally as well as transversely (*fig.* 98. *a*), and its angle with the spine marked 160°. There are generally four sacral vertebræ, but the first is much larger than the others, especially in its lateral masses (*b*), to articulate with the ilia. The Rabbit and Jerboa, however, present only two; and the common Rat and Beaver three; while the number in the Marmot is as many as six. The spines are not coalesced except in some Rats. The *caudal* vertebræ are more or less numerous, and are remarkable in the Beaver for the great length of the transverse processes and anterior spines, for muscular hold on this its useful appendage. In the Squirrel and Jerboa also, the tail is long and strong, and in the habitual sitting posture of these animals it forms, with the ischia, the third leg of a tripod, on which the body is sustained. In the short-tailed Rodents, the caudal vertebræ are curved dorsally, in an opposite direction to the coccygeal bones in Man and the *Simiæ*.

The *ilia* are long, prismatic, and slender in the shaft, having a central ridge passing upwards from the cotyloid cavity, with a groove on each side of it externally, and continued forward into elongated alæ, little more expanded than the shaft in most of the order. They form with the spine an angle of about

Fig. 98.



Pelvis of the Hare, anterior view.

165° in the Hare, and 150° in the Porcupine. In the Copyrus, Rats, Mice, and Guinea-pig, they are nearly parallel with the spine; but in the Jerboa they *cross* the spine at an angle much less than in others, being about 140°. In the Jerboa the iliac wings are curved outwards superiorly and projected much on the dorsum of the spine, reaching beyond the elongated spines of the last lumbar vertebra. The ilia of the Beaver, and, in a less degree, in the Hare, are expanded, with prolonged and irregularly curved crests (*c*), a little everted at the spinous processes (*g*), and proportionally short in the shaft. The *ischia* in Rodents are generally long, especially in the Beaver and Jerboa. In the latter animal they are directed much outwards, with tuberosities large, much expanded, and everted posteriorly, to give firm attachment to the strong sacro-sciatic ligaments. They are placed in a right line with the ilia, the ilio-ischial angle being wanting as in the *Carnivora* (*see fig.* 112. 8.). In the Hare the tuberosities of the ischia are large, and present well-marked lateral processes (*e*), which are everted, and rise above the level of the coccygeal vertebræ. The *pubes* are long and slender, and generally join with the ischia in a long median symphysis projecting in a sharp, anterior, vertical, ridge (*f*); except in the Porcupines, Rats, and Mice, which have a short symphysis pubis. In the Jerboa there is a slight *pubic spinous process*, very externally placed; this is better marked in Hares (*d*), Rabbits, and Beavers. The *ilio-pubic* angle in Hares and Rabbits is about 120° to 130°. In the Jerboa it is more oblique, 145°; and still more so in Rats and Mice, 150°.

The sciatic notch is generally long and narrow, especially in the Jerboa; and the obturator foramen very large, particularly in the Beaver. The pelvic cavity and outlets are large and capacious, especially in the Jerboa, in which, by the outward direction of the ischia, the posterior outlet is much larger than the anterior. In the Beaver also the transverse pelvic diameter is large, and separates widely the hinder extremities of these animals, to aid their swimming habits. In the Capybara however, the pelvis is of little capacity.

In the Guinea-pig it is compressed so much *laterally*, that the anterior opening is of a triangular shape, with the apex at the pubic symphysis. According to Le Gallois, it measures only 11 millimetres transversely in a full-grown female, while the fœtal head measures 20 millimetres across. Three weeks before labour begins, the elastic ligament uniting the symphysis pubis becomes thick, soft, and moveable; and eight to ten days before, the pubes, turning on the sacro-iliac joints as on a hinge, begin to separate rapidly, till the time of parturition, when they admit one or two fingers between them. After accouchment, the symphysis quickly returns to its original condition, and in a few days presents only a little thickness and mobility, the process being delayed only by age and sickness. Le Gallois found the sacro-iliac symphysis also very moveable, so as to allow of the retreat of the sacrum, and the increase of distance between its extremity and the pubic symphysis when the fœtal head pressed upon it. In this manner the pelvis of the Guinea-pig is widened, during labour, in all its diameters. Its young are produced in a very advanced state of development, and are able to run about and eat as soon as they are born.

In the *Marsupialia* the pelvis is also much developed, both to afford attachment to the powerful muscles of the tail and hinder legs, and, in some of the order, to support the abdominal viscera in their sitting posture and leaping movements. It is remarkable for the development, in most of the genera, of two extra bones (*fig.* 99. *a.*) characteristic of the order, which are attached to the pubes in the site of the crests and spines of these bones in other animals, and support the abdominal pouch peculiar to them and destined for the reception and more mature development of their young, expelled immature from the pelvic cavity. They are directed obliquely forwards and a little outwards, in the direction of the fibres of the aponeurosis of the external oblique muscle of the abdomen; in which, according to Owen and Laurent, these bones are developed by ossification of the fibrous tissue. The free extremities are a little curved, and over them the cremaster muscles in the male animals play. The pelves of the Marsupials differ considerably, according as the mode of progression is quadrupedal, or by a succession of springs from the tail and strong hinder extremities. The Wombat may be taken as an example of the former, and the Kangaroo of the latter pelvic type, which approaches in general form to the pelvis of the Jerboa, just considered.

The *sacrum* of the Wombat is very flat, and strong, and broad, in correspondence with the general squat and massy skeleton of the animal (*see figs.* 102. and 108. Art. *Marsupialia*). Its curve is a continuation of that of the dorsal and lumbar vertebræ. The number of sacral vertebræ is seven, and the transverse processes are separated from each other, the three upper of which are long and strong, and are articulated by their tips to the ilia. The facet on the extremity of the first looks *upward* and outward, and that on the second, on the contrary, *downward* and outward, and form projections which impinge upon the iliac facet. This arrangement in the Wombat like that in the Tapir, is closely analogous to the formation of the sacral "joggles," and the alteration of the inclination of the sacral wedge in Man, at the point of the auricular surface opposite the second sacral piece, substituting for upward, *backwards*, and for downward, *forwards*, a change consequent on the difference between the prone and erect positions. *Caudal* pieces are numerous.

The *ilia* are comparatively short and expanded considerably, and are curved outwards in a remarkably strong, broad, hook-like process at the anterior superior spine. They are placed very obliquely on the spine, being at an angle of 160° with the lumbar portion of the great dorsal curvature. The *ischia* are thick, long, and massy, and in a right line with the ilia. They have curiously bifurcated tuberosities, one tubercular projection turning inward, and the other longer, curving outward, in another remarkable and strong hook-like process, to which formation we have before remarked a tendency in the Hare and other Rodents (*fig.* 98. *e*). These processes, like those on the ilia, afford a powerful hold and leverage to the strong muscles of the hinder extremities, much used by the animal in its burrowing habits. These hook-like processes of the ischia are formed by a Y-shaped apophysis analogous to that of the tuberosity in man. The *pubes* are short and thick ; and the symphysis is parallel to the spine, very long, and joined in very extensively by the vertically directed rami of the ischia.

The *marsupial bones* of the Wombat are long, flat, rounded and expanded at their free extremities, and articulated to the anterior border of the pubes in the position of the crests by two articular facets separated by an arched interval. Ilio-pectineal spines are present, and of large size.

The whole pelvis of the Wombat is large and massy, though the openings and outlets are proportionably very small. It has a flattened appearance antero-posteriorly, so that the anterior outlet has its greatest diameter transversely placed.

In the *Myrmecobius fasciatus* this flattened appearance of the pelvis is still more remarkable.

In the Opossums, *Perameles*, and Phalangers, there is but one sacral vertebra, which, in the *Phalangista Cookii*, is ankylosed to the last lumbar vertebra.

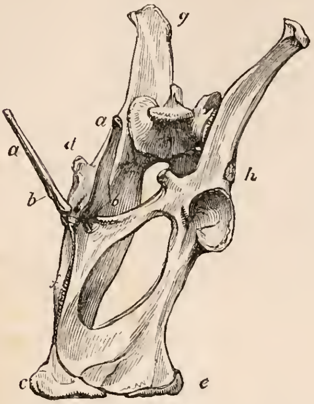
The pelvis of the *Thylacinus Cynocephalus* approaches closely in many respects to the type of the *Carnivora*, like many of the peculiarities of this animal. The *sacrum* presents no angle ; the *ilia* are massy, somewhat short, and less oblique than those of the Wombat : the *ischia* are also short and thick, and are placed at an open angle (170°) with the ilia, while the pubes are short and directed almost horizontally inwards, making an *antero-posterior* angle with the ilia as little as 115°. The whole appearance of the pelvis is massy, with small openings. It has neither the oblique appearance and exaggerated processes of the Wombat, nor the elongation and wide outlets of the Kangaroo, while its well-marked *ilio-pubic angle* contrasts much with both, and shows a strong similarity to the *Carnivora*.

In the Kangaroos, the *sacrum* is in the line of the lumbar curve, and differs in little but size and breadth from the preceding vertebræ. There are two sacral vertebræ, articulating with the ilia, their transverse processes being long and coalesced, but the spinous processes distinct. In the Potoroo there is one only, with large lateral processes. The *caudal* vertebræ are numerous and very strong, and their upper normal spines encroach much on the diameter of the pelvic cavity and posterior outlet. The *ilia* have short, strong, and prismatic shafts as in the Rodents, with alæ of the same shape, much elongated and turned outwards, though in a much less degree than in the Wombat, and terminating in narrow clubbed crests (*fig.* 99. *g*). There is a rudimentary inferior anterior spine (*h*). The upper part of the iliac wing projects much on the dorsal aspect of the spinal column, forming with it an angle of 140° (see *fig.* 112. 9.). The *ischia* are very long, broad, and strong, and have much-expanded tuberosities with an outward curvature (*fig.* 99. *e*). These are united in a median symphysis by a single V-shaped epiphysis (*c*), divided, in the adult, by a suture from the ischia. The tuberosities support also another epiphysis on each side posteriorly at *e*, the anterior ischial rami being almost deficient. The ilia and ischia are very nearly in a direct line. The *pubes* are moderately long, slender, and directed much downward, so as to give to the anterior outlet a triangular shape, with the base at the broad sacrum, and the apex at the pubic symphysis. The *ilio-pubic angle* is 135°.

The *marsupial bones* (*a*, *b*) are smaller, rounder, and more curved externally than in the Wombat. Their free extremities are tuberculated and not flattened, and they are articulated to the pubic crest near the symphysis by a single facet only, the inner, the position of the outer one being marked by a slight tubercle (*b*). The ilio-pectineal spines (*d*) are very large, for the attachment of powerful psoæ muscles.

The direction of the ischio-pubic symphysis (*f*) in the Kangaroo, *Phascogale*, and Potoroo, is not parallel with the spinal column, but

Fig. 99.



Pelvis of the Kangaroo, showing the marsupial bones (a á) and inter-sciatic epiphysis (e).

oblique in the opposite direction to the human symphysis, so that if prolonged forwards the line of direction would cut the spinal column at an obtuse angle. This makes the posterior opening larger in its antero-posterior diameter than it otherwise would be, and allows for the great encroachment of the caudal vertebræ posteriorly. The sciatic notch is long and narrow, corresponding to the great length of the ischia; and the foramen obturatorium is large and elongated antero-posteriorly from the same cause. In the *Dasyurus* and *Petaurists*, the ischio-pubic symphysis is oblique in the opposite direction. The antero-posterior diameter of the anterior outlet in the Kangaroo is greater than the transverse by about half an inch; but at the posterior outlet, the transverse is a little greater, from the projection of the caudal spines before mentioned. The pelvic *cavity* is deep in the *Marsupialia*, and its openings are small in proportion to the size of the animal, since the fœtus is expelled before it is full grown, and placed on the nipples in the marsupial pouch to complete its development into a state of independent existence. But the proportion between the pelvic openings and the size of the fœtal head, at the period of expulsion, is very remote. Even in the *Petaurists*, whose pelves are the smallest, the cavity and openings are six times the size of the fœtal head.

The muscles of the tail and legs attached to the pelvis are, in the Kangaroos, very powerful to perform their prodigious leaps, especially the gracilis and biceps. The glutei, however, are not large, since the trunk is not held erect on the legs by these muscles, but is suspended, as it were, between the femurs, and supported in front by the largely developed psoæ muscles, and behind by the powerful tail, used as a propelling organ by the sudden action of its flexor muscles.

The pelvis of the *Monotremata* resembles in general appearance the reptile type, although in some other respects these curious animals, especially the *Ornithorhyncus*, approach the Birds. The *sacrum* of the *Ornithorhyncus* is composed of two vertebræ, separated, as in the Saurian reptiles, and placed in the line of the lumbar curve, differing little in appearance from the lumbar vertebræ. In the *Echidna* are three sacral vertebræ, also separated and all uniting with the ilia.

The *ilia* are short, thick, and prismatic, and project above the spine at an angle of 140° as high as the sacral spines, and presenting, in the *Ornithorhyncus*, considerable eversion of the alæ, and, in a much less degree, in the *Echidna* also. The *ischia* are short, bent upwards in the former, and project backwards at the tuberosities in an angular spine, most marked in the *Ornithorhyncus*, and giving a reptile-like appearance. The *pubes* are broad and short, placed at a marked angle with the ilia, 110° in the *Echidna hystrix* and 120° in the *Ornithorhyncus*, and uniting by broad plate-like rami with the ischial rami, which form with them a long ischio-pubic symphysis. The ischio-pubic plate thus formed is very like that seen in the reptiles.

The *marsupial* bones are also present, and are very large and strong in this class, although not provided with a pouch. In the *Ornithorhyncus* they are broad and triangular, articulated by the base to the whole length of the pubic crest meeting in the median line, and with their rounded apices directed forwards and outwards. In the *Echidna* they are longer, rounder, more pointed and less everted, with two articular processes at the pubic extremity (*see fig.* 177. Art. *Monotremata*).

The ilio-pectineal spines are also very large in the *Ornithorhyncus*, and in a less degree in the *Echidna*. The obturator foramina are small. The three pelvic bones are united at the cotyloids by bony union in the *Ornithorhyncus*. In the *Echidna hystrix*, the union of these bones is, however, effected by cartilage only, and the acetabula are perforated by a considerable opening into the pelvic cavity, constituting another remarkable reptile-like peculiarity.

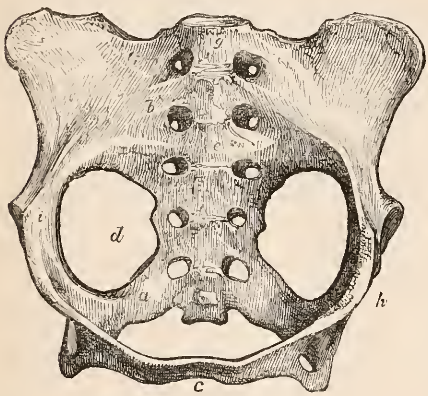
Having traced the Mammalian pelvis to a form presenting somewhat of the reptile type in the Monotremes, we may now recur back to an order of animals which, from their general organisation, are connected closely to the order of primates, and are usually placed much higher in the animal scale than the position here assigned to them.

These are the Sloths or Tardigrades, which form the connecting link between the *Simiæ* and *Edentata* proper. Their pelvic peculiarities, however, ally them more closely to the Birds. The most striking of these is the ossification of the ilia and ischia to the broad sacrum, by transformation of the sacro-iliac and sacro-sciatic ligaments. We have already noticed an exceptional example of this coalescence in the Ruminants, in the *Meminna* or pigmy Chevrotain. But the pelvis of the *Edentata* also presents a diminution of the pubic symphysis, and the absence of the ischia from this junction, a separation which is carried still further in the *Insectivora* and *Cheiroptera*. The increasing obliquity of the pubes also indicates an approach to the Bird type.

The climbing habits of the Sloths produce a habitual vertical position of the trunk, requiring for the support of the abdominal viscera large open pelves.

In the Ai (*Bradypus tridactylus*) the pelvis (*fig*. 100.) is remarkably slender, expanded, shallow and horizontal in direction, the pelvic openings being very large and round, and the antero-posterior diameters little larger than the transverse. The ankylosis of the innominate bones to the sacrum in these animals gives a great firmness to the support of the otherwise feeble hinder extremities, and with the great distance of separation of the acetabula, which are small and shallow, assists to a considerable degree their climbing and holding powers, and to produce that slowness and awkwardness of motion which has given them the name of *Tardigrades*.

Fig. 100.



Pelvis of the Ai, anterior view.

The *sacrum* is large, both in length and breadth, very flat, with large, open foramina, and presenting a flattened surface in place of the posterior spines and tuberosities. It is composed of five vertebræ, of which the three upper (*e*) as well as the last lumbar (*g*) are ankylosed to the ilia (*b*). The union of the last lumbar seems to result from an extension of ossification in the ilio-lumbar ligament (*i*), and contributes much to increase the steadiness of the spinal column on the pelvis. The *coccyx* is triangular, little curved, broad and short, and is composed of six pieces. In some species it is prolonged into a tail.

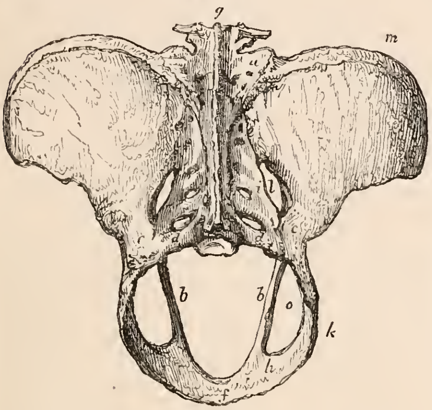
The *ilia* are short and slender, with much-expanded wings, having an anterior concavity and a plane surface posteriorly. They are ossified to the sacrum at an early period. The *ischia* are short and slender, and united to the last sacral vertebra, and more slightly to the two above it, by ossification of the great sacro-sciatic ligament (*a*), which gives to the angle of the bone an expanded appearance, and encloses a round, wide *sacro-sciatic foramen* (*d*), above and behind the cotyloid cavity. The tuberosities are small, and the inferior rami (*f*) are long and slender, enclosing with the pubis a very large obturator foramen, having its long diameter from side to side, and do *not* join in symphysis. The *pubes* (*h*) are long and slender, their rami united in a V shape, with the angles meeting to form a very short symphysis (*c*), which is sometimes ossified, and presenting a very slight ilio-pectineal spine (*i*). The *lumbo-iliac angle* in the adult *Bradypus* is about 145°, and the *ilio-pubic* about 155°, being only about 25° from a right line as in the human pelvis. The *ilio-ischial angle* also approaches the human standard in being diminished to 135°.

This diminution of the *ilio-ischial angle* is still more remarkably shown in the *Mylodon* and *Megatherium* fossil gigantic Sloths, which approach more closely to Man in this respect than any other Mammalian.

The osseous system of the fossil *Mylodon robustus* closely resembles that of the Sloths, differing from them, however, by presenting a continued sacral crest, and more expanded ilia (*fig*. 101.). According to Professor Owen, in his valuable monograph on the specimen in the Hunterian Museum, the *sacrum* really consists of seven vertebræ, but by ankylosis with the three lumbar and last dorsal includes eleven vertebræ, and forms one strong and continuous bony mass along the whole lumbar region (*a*). Its total length is 2 feet 4 inches, and it gradually increases in breadth to the sacro-iliac union (*e*), which is formed by the first, second, and third true sacral vertebræ, and there presents its greatest breadth. It then contracts slightly, and, at the sixth and last, expands again to join the ischia (*d*). It is firmly united by ankylosis both to the ilia and ischia. Its anterior surface is curved both laterally and vertically. The spinal canal is very wide, and the foramina passing from it mark the primary vertebral divisions. The whole of the eleven spinous processes of the ankylosed vertebræ form a remarkable curved crest posteriorly (*g*). There are twenty-one *caudal* vertebræ, which doubtless, in the living animal, contributed to support the body by application to the limbs of the trees upon which it climbed, and were strongly supported by the sacro-sciatic ossification.

The *innominate bones* are very large. The iliac wings are much spread out, widely concave anteriorly, and slightly convex posteriorly, these surfaces being directed forwards and backwards. The iliac crest presents a continuous, well-arched curve, and at the inner part of its centre (*m*) it is prolonged and curved forward in a lip which overhangs the anterior fossa, and contributes to support the bulky viscera. The lips of the crest are remarkably spread. The posterior superior spine is continued by an oblique crest of bone (*a*) to the lateral tubercles of the lower sacral vertebræ, as if from ossification of the oblique sacro-iliac ligament. The posterior inferior spines are continued by a ridge to the borders of the fifth, sixth, and seventh sacral pieces into the bony ankylosis of these with the ischia, which are ankylosed to the same parts, evidently in the position of the sacro-sciatic ligaments (*d*). The *ischia* (*c*) are comparatively short and directed obliquely backwards and downwards, and have remarkably slender tuberosities, as is the general characteristic of the Sloths. The inferior rami (*k*) slope much forwards, and join with the pubis in a plate of bone (*h*) before reaching the symphysis (*f*), which is very narrow and formed by the pubes only. The *pubes* (*b*) of the Mylodon are long and very slender, and form an angle of about 160° with the ilia, the apex of the angle being directed *forwards*, a remarkable peculiarity, by which it differs, in common with the Ant-eaters, from the other Mammalia. The *vertebro-iliac* angle is rather acute, being about 125°, and the *ilio-ischial* is as small as 120°, being very near the human angle.

Fig. 101.



Pelvis of the Mylodon robustus, posterior view; showing the ossification of the sacro-iliac and sciatic ligaments.

The whole pelvis is remarkable for its breadth and shallowness. The anterior outlet is of an oval form, with the long diameters antero-posterior. The posterior opening is somewhat pentagonal, and, from the great antero-posterior direction of the ischial rami and the ossified sacro-sciatic junction, presents a flat level rim. The sacro-sciatic foramen (*l*) is comparatively small, but the obturator foramen (*o*) is large and oval.

The pelvis is one of the most characteristic parts of the fossil *Megatherium*, as forming the fulcrum of muscular forces of unusual vigour. The *sacrum* is very narrow, and shorter proportionably than in the Mylodon, and is composed of five vertebræ, only the last being broader transversely. There is no ankylosis to the last lumbar vertebra.

The *iliac wings* are large and expanded, with a concavity directed forwards, the anterior superior spines overhanging the femurs, and the external border very concave. They are more massy than in the *Mylodon*, and present no hook-like process on the crest. The *ischia* are broad, blade-like, and massy; the tuberosities are not well marked, but rounded and ankylosed to the lower sacral vertebræ, enclosing a small foramen, and contributing, with the ankylosed ilia, to support the weight of the animal. *Ilio-ischial angle* 125°. The *pubes* are slender and very oblique, and form, like the Mylodon, a *reversed ilio-pubic angle* of about 155°. The pubic symphysis is narrow, and presents anteriorly a rostrated projection. The acetabula are large and near to each other; the planes are inclined from the perpendicular about 65°. The anterior outlet is oval, with long diameter antero-posterior. The posterior has the long diameter transverse. The obturator opening is comparatively small. The whole pelvis has a very massive appearance.

The pelvis of the other *Edentata* presents the same general type as that of the Sloths.

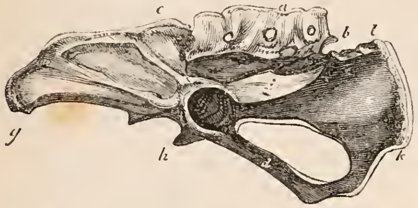
In the Armadillo (*Dasypus longicaudus*) there is a *sacrum* of nine vertebræ, the three upper of which are ankylosed to the ilia, and the sacral spines are coalesced in a crest. The sacrum is narrowed to a remarkable extent between its iliac and its sciatic portions, expanding much in the latter part to meet and coalesce with the ischia, with which it forms a broad osseous plate in the site of the sacro-sciatic ligaments. The oblique sacro-iliac ridge is also well marked. The *caudal* bones are numerous.

The *ilia* are long, strong, broad, and prismatic, and the alæ are prolonged into broad lamellar plates, which are ankylosed continously to the sacrum, and assist to support the carapace. The ilia are much more approximated to each other than the ischia. *Lumbo-iliac angle* 155°. The *ischia* are large, broad, and considerably divergent, with broad tuberosities prolonged dorsally to support the shell; coalescing in a broad plate with the lower sacral pieces, and enclosing a moderately sized *sacro-sciatic foramen*. The rami are at right angles to the body of the ischia. The *ilio-ischial angle* is marked, (145°). The *pubes* are slender and very obliquely directed backwards, making an *ilio-pubic angle* of 150°; and the symphysis is short, especially in the Weasel-headed Armadillo, in which also the *ilio-pubic angle* is smaller. (130°). The posterior pelvic outlet is much larger than the anterior, from the greater eversion of the ischia.

In the Cape Ant-eater (*fig.* 102.) the *sacrum* is composed of six pieces, with the spines (*a*) coalesced, but leaving foramina between them, and the last transverse processes (*b*) elongated. *Caudal* bones numerous (*fig.* 102.).

The *ilia* are very thick and prismatic, and more perpendicular to the spine, with the anterior and posterior borders thickened into a strong ridge. The alæ are concave externally, the posterior superior spines (*c*) prolonged dorsally, and ankylosed to the sacrum, and the anterior superior (*g*), prolonged and curved outwards and downwards. The *ischia* are very long, expanding into a broad plate posteriorly (*e*), but do not touch the last sacral vertebra. The ischial spines (*i*) are marked, and the tuberosities present two tubercular projections, one directed outwards, long and sharp (*k*); and the other thicker, and directed dorsally (*l*). The *pubes* (*d*) are directed obliquely backwards with very short symphysis (*f*), and the ilio-pectineal spine (*h*) is very large. The pelvis is altogether massy and large, with long sciatic notches and considerable obturator foramina.

Fig. 102.



Pelvis of the Cape Ant-eater, side view.

In the great American Ant-eater, both the ilia and ischia abut closely on the sacral transverse processes, presenting a faint suture at the line of junction. The pelvis is proportionately smaller and lighter, and the processes and spines much less marked than in the Cape Ant-eater. The *lumbo-iliac angle* in the Ant-eaters is 140°, the *ilio-ischial* 140° ; and the *ilio-pubic* is *reversed*, and about 155°.

The Manis possess pelves of the same general heavy appearance as the American Ant-eater. The *ilia* and *ischia* are closely approximated, but not ankylosed to the *sacrum*. The symphysis pubis is short and not joined by the ischia, and the pelvic openings comparatively small.

In the foregoing Sloths and *Edentata*, and in some of the Rodents, we have remarked the tendency of the anterior symphysis to become shorter and more imperfect by the absence of median union of the ischia, and that this is accompanied by a corresponding increase of the bond of union between the sacrum and ilio-ischian elements of the pelvis, by a closer approximation or ossification of their uniting ligaments, to give greater firmness to the pelvis as its anterior connection fails.

In the *Insectivora* and Bat tribe, this separation of the innominate bones is increased, and the pubes also fail altogether, in many instances, to meet in the median line. By the classification of animals according to their pelvci development, which is here adopted, these tribes are placed much lower than their general osteology allows, in the general classification commonly given by authors, and are allied more closely to the Bird type in their pelvic formation.

Of the *Insectivora*, the Hedgehog presents the least pelvic departure from the common mammalian type. The *sacrum* is narrow and triangular, and composed of four vertebræ, three of which articulate with the ilia. The *ilia* are thin and elongated, and placed on the spine at an angle of 130°. The *ischia* are slender, projecting above the level of the sacrum, but not touching it ; and the rami are long and slender, and enclose with the pubes large obturator foramina. The *pubes* are long, slender, and obliquely directed, making an *ilio-pubic angle* of about 150°. The symphysis is very short, and the pelvic outlets large, with the long diameters antero-posterior.

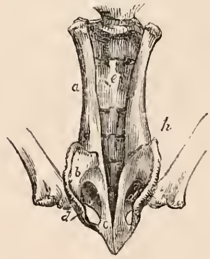
In the *Tupaia*, one *sacral* vertebra only, out of three, unites with the *ilia*, and there is a good sized symphysis pubis, as is also seen in the Tenrecs. In the genus *Desman* two *sacral* vertebræ articulate with the *ilia* and one with the *ischia ;* and the *pubes* are very obliquely placed on the ilia, and, according to Blainville, are placed, anteriorly, rather in contiguity than in symphysis, giving to the pelvis very much of the appearance of that of the Ostrich. In the *Macroscelides* there is a short and rudimentary pubic symphysis.

The Mole (*Talpa*) and the Shrews (*Sorex*) are remarkable for a very narrow *sacrum*, composed, according to Blainville, of four vertebræ, but, according to Cuvier, of seven in the Mole and three in the Shrews. In the Mole the ilia are solidly ankylosed to nearly the whole length of the sacrum. In the Shrews the two first only of the sacral pieces are united with the ilia. The spines in both are coalesced into a prominent sacral crest. *Caudal* pieces numerous.

The *ilia* are cylindrical, much approximated, and parallel to the spinal column. The *ischia* are much elongated, and elevated posteriorly above the sacral vertebræ. The *pubes* are very short and slender, and though they unite with the short ischial rami to enclose a small obturator foramen, do *not* meet in a symphysis, but present an anterior interval, said to be wider in the female than the male, and causing the whole pelvis to assume very much a bird-like appearance. The pelvic cavity and outlets are so strait that the sexual and urinary organs and rectum pass altogether in front of it.

In the Bats (*Cheiroptera*) the *sacrum* (*fig.* 103, *e*), is very narrow, compressed posteriorly into a straight continuous bone, with no lateral foramina, and composed of three to four vertebræ, which are joined by ankylosis to three or four upper coccygeal vertebræ, or to more in the tailed species. There are six to twelve *caudal* bones, sometimes absent, as in *Pteropus* and Vampire.

Fig. 103.



Pelvis of the Ternate Bat (natural size), anterior view ; showing the inter-pubic separation (*d, d'*).

The *ilia* (*a*,) are narrow and subcylindrical, with a thick anterior spine, placed parallel to the vertebral column, and *ankylosed* to the anterior sacral vertebræ. The *ischia* (*c*) are in the same right line with the ilia, and are ankylosed at the tuberosities with the last sacral vertebræ, and, as seen especially in the Ternate Bat, given in the above figure, presenting an appearance as if ankylosed to each other in one mass, from the extreme narrowness of the sacrum at that part, inclosing a small *sacro-sciatic foramen*. The *pubes* (*b*) are thick, short, and very oblique, joining with the short ischial rami at *d*, to form an elongated obturator foramen (*f*). The ilio-pectineal spine (*h*) is very prominent, and recurved almost like a marsupial bone. This is especially seen in the *Vespertilio spectrum*, in which it is considered by Wagner as the first indication of a marsupial bone. The pubic symphysis is totally wanting generally in the Bat tribe, leaving a large interval (*d*, *d′*) ; but, according to Pallas and Schreger, the males of some species possess a symphysis, which is wanting in the female, a peculiarity curiously illustrative of the influence of sex on the pelvis. In a specimen in the Hunterian Museum the symphysis, or a close approximation of the bones, is certainly present, though very short. The cotyloid cavities in the bats are closely approximated, and are directed *backwards* as well as outwards, causing the retroversion of the feet seen in these animals. The pelvic cavity and outlets are much more capacious than in the Mole and Shrew.

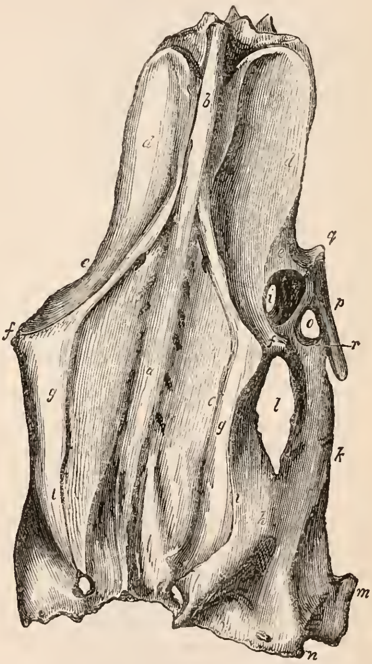
In the *Cetacea*, which are in other respects osteologically allied to the *Pachydermata*, the pelvic development suddenly becomes degenerated into small elongated bones, which may be considered as the homologue of the *pubes*, and which are imbedded in the muscles of the abdomen immediately in front of the ventral opening, and give attachment to the *crura penis*. They differ, only in being thicker and less transparent, from the pelvic bones of the true Fishes, between which and the Mammalia these animals are the connecting link, as the Bats to the Birds, and the *Monotremata* to the Chelonian reptiles.

In the Dolphins these pubic bones are two simple, elongated, flat bones placed on each side of the median line. In some Whales they are connected by a cross piece, and assume a hyoid shape (*see fig.* 257. Art. *Cetacea*). In the Dugong it is a V-shaped bone formed of four pieces, and articulated to one of the vertebræ by its free extremities. In the *Manatus*, according to Carus, they are entirely wanting.

The pelvic structure of *Birds* is characterised by very evident distinctions from the mammalian type, the osseous parts being accumulated, as it were, on the posterior and lateral parts, leaving the anterior parietes deficient, and being also thinner and more spread out, so as to leave smaller foramina.

The *sacrum* (*fig.* 104. *a*) is generally broad and large, consisting of from eight to twenty pieces, being increased forwards by ankylosis to the vertebræ corresponding to the lumbar region of the Mammalia, and which contribute to support the iliac wings. This arrangement, as well as the extensive ankylosis of the ilia and ischia, has an evident relation to their bipedal support, and is compensatory for the deficiency of the pelvic circle anteriorly. It is much more extensive in the *Cursores* and those which use the legs as the most usual instruments of progression. The bodies of the sacral vertebræ are raised in a continuous ridge on the anterior aspect, those immediately between the acetabula being larger and broader than the rest (*fig.* 105. *a*). The first five or six (*s*), which may be considered as the ankylosed lumbar vertebræ, present marked spinous processes united in a high crest which intervenes between, coalesces with, and supports the iliac wings at their inner margins (*fig.* 104. *b*). Their transverse processes, which are also ankylosed to the ilia near their outer borders, are strong and well marked on the ventral surface, and differ from those of the true sacral vertebræ in being more prominently advanced and having a direction more horizontally outwards instead of backwards and upwards (*fig.* 105. *r*), the most posterior being the thickest and placed at the junction of the iliac wing with the shaft. A

Fig. 104.



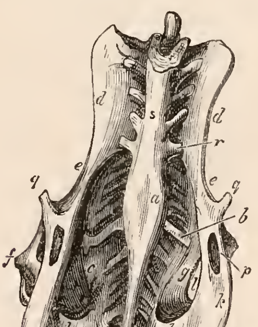
Superior or dorsal aspect of the pelvis of the Duck: *a*, sacrum; *b*, coalesced lumbar spines; *c*, sacral suture; *d*,' ilium; *e*, cotylo-sacral rib; *f*, ischio-sacral buttress; *g*, sacro-iliac plate; *h*, sacro-sciatic plate; *i*, acetabulum; *k*, ischium; *l*, sacro-sciatic foramen; *m*, rudiments of ischial ramus; *n*, spine; *o*, anterior obturator foramen; *p*, pubis; *q*, ilio-pectineal spine; *r*, anterior ischio-pubic union.

little anterior to the acetabula, however, where the true sacral vertebræ may be considered to commence, the spines gradually become less marked as they emerge from between the iliac wings and form a more or less flattened surface (*a*), which is separated from the coalesced transverse processes by two faintly-marked longitudinal grooves. The transverse processes of the true sacral vertebræ present a very prominent framework of ridges anteriorly (*fig.* 105.), which have a direction upwards and backwards as well as outwards, the most strongly marked being opposite the acetabula (*b*). They are coalesced on the superior aspect, by a thin plate of bone only. The sacrum, as seen from above (*fig.* 104.), has a diamond-shaped appearance, and is marked out from the iliac and ischial elements by a faintly-marked suture (*c*). The sacrum in Birds is a continuation of the line of the great dorsal curvature.

The *coccyx* is generally short, composed of from five to nine pieces, generally perforated for the spinal marrow, and curved dorsally, as we have observed before in some Rodents, terminating in a spinous-shaped piece (*see fig.* 107., *a*).

The *ilia* are comparatively short and narrow: with a very short cotylo-sacral rib or shaft (*e*), directed upwards and forwards, and expanding into a wing (*d*), concave or grooved superiorly. *The ala* is prolonged forwards on the posterior surfaces of the ankylosed lumbar vertebræ, coalescing with their spines and transverse processes; and also extends backwards to a less degree, to coalesce with the upper bifurcation of the anterior extremity of the ischium, in a sort of *buttress* (*f*), which projects externally and overhangs the acetabulum posteriorly, presenting, below, a facet, against which rests the trochanter of the femur, and which is apparently a continuation of the articular cotyloid surface. This buttress is continued from the ischium inwards, as a strong ridge, to the extremity of the strongest of the sacral transverse processes before mentioned (*fig.* 105. *b*), opposite the

Fig. 105.



Inferior or ventral view of the pelvis of the Partridge—natural size: *a*, coalesced bodies of sacral vertebræ; *b*, sacral transverse processes; *n*, ischial spine; *r*, lumbar or pseudo-sacral processes; *s*, ankylosed lumbar vertebræ. The remaining letters refer to the same parts as in *fig.* 99.

lateral angles of the diamond-shaped sacral plate, and evidently contributes in the greatest degree to support the trunk upon the femurs in the standing posture. The principal part of the ilium in birds is composed of the alæ, which lie almost altogether on the dorsal aspect of the spinal column. The total axis of the ilium, however, crosses that of the spine at an angle of from 150° to 160°, and does not, strictly speaking, lie parallel to it, as is commonly asserted (*see fig.* 112. 10.).

From the posterior part of the inner border of the iliac wing passes backward a thin *plate of bone* (*g*), along the external borders of the diamond-shaped sacral plate, from which it is marked by a distinct line of suture (*c*). It is continuous, posteriorly and externally, with the sacro-sciatic ossification, to be presently mentioned, from which it is also marked, especially in the Partridge and some other birds, by a raised line of demarcation (*t*). This thin plate is convex above and concave below, and enters into the formation of the pelvic cavity, being much hollowed in the Partridge and the *Gallinaceæ* generally (*fig.* 105. *g*), to receive the pelvic viscera. It seems to result from the ossification of the sacro-iliac oblique ligament, and to form a separate pelvic element which may be called the *sacro-iliac*, or *ilio-sacral*.

The *ischia* of birds (*k*) are long, strong, and divergent posteriorly; and, from the perforation of the cotyloids, appear to be bifurcated at the anterior extremity. The inferior bifurcation is horizontal, coalesces with the ilium and pubis, and separates the acetabulum (*i*) from the obturator foramen (*o*). The superior bifurcation is vertical in direction, separating the acetabulum (*i*) from the sacro-sciatic foramen (*l*), and coalescing above, internally with the long sacral transverse process (*b*) and ilio-sacral bone (*g*), and anteriorly with the ilium in the *ischio-sacral buttress* (*f*), before mentioned, which it principally contributes to support and form, and which may be considered as the homologue of the *ischio-sacral* arch in the human pelvis, separated from the *cotylo-sacral rib* (*e*) by a thin plate of bone above, and by the perforated acetabulum below. The posterior extremity of the ischium is much elongated, and constitutes the bulk of the bone. Its inferior border is spread out into a broad thin plate, slightly prolonged into an anterior process (*m*), which seems to represent the ascending ramus of Mammals, from its frequently uniting with the pubis and forming the posterior boundary of an obturator foramen.

Its superior border is prolonged into a broad thin plate (*h*) hollowed out in the pelvic cavity, and which constitutes the *sacro-sciatic pelvic element*, being evidently formed by ossification of the sacro-sciatic ligaments, from its completing posteriorly the *sacro-sciatic foramen* (*l*), and coalescing with the *sacro-iliac* plate (*g*), before mentioned, and, behind it, with the sacrum. The posterior extremity of the ischium is prolonged generally into a thin angular spinous process (*n*). The *ischia* in Birds generally form a right line with the ilia; but in the *Birds of prey* they constitute a remarkable exception, and make a very marked *ilio-ischial angle* in the reverse direction to that of Mammals generally, *i. e.* with the retiring sides anterior (*see fig.* 107.).

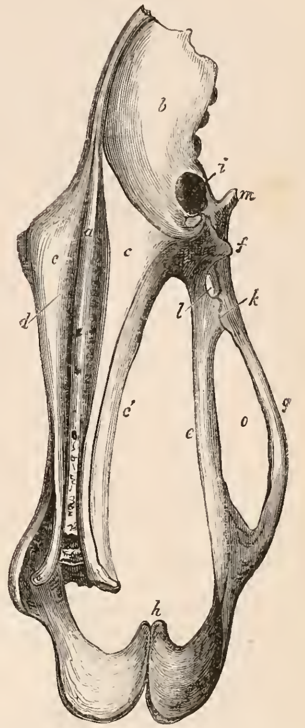
The *pubes* of birds are generally long, slender, rib-like, and divergent, and are composed of a single curved branch (*p*), having no angle, and never forming a true interpubic symphysis, though, in the Ostrich and Falco Fulvus, they are closely approximated at their posterior extremity, and form a sort of symphysis. The *ilio-pubic* angle is very large, from 155° to 160°, except in the birds of prey above alluded to ; and the pubes and ischia are generally almost parallel. Sometimes the posterior extremities of the pubes and ischia unite to form complete elongated obturator foramina ; and they may be united also near their anterior extremities, forming a lesser anterior division of the foramina, as in the *Cursores* (*see fig.* 106. *k*). Very often, the boundaries of the obturator openings are incomplete from the failure of this junction, and the foramina are wanting altogether ; or the anterior union and foramina only may be present, as in the Duck (*fig.* 104. *r*), from deficiency of the pubes posteriorly, or their entire approximation to the ischia. The pelvic cavity is increased in size posteriorly, by the divergence of the pubes and ischia, and is capable of great enlargement by the yielding of their unfixed extremities. The ilio-pectineal eminence is generally present, and often large in size, constituting a spinous process (*q*). The *acetabula* (*i*) are perforated and placed almost close to the borders of the sacrum, and generally much anterior to the centre of the whole pelvic length, that the points of support may be nearer the centre of gravity.

The bird's pelvis thus constitutes a firm, compact, immobile, box-like structure, deficient inferiorly, affording a large and firm hold, by the elongated and strong ischia, for the extensor muscles of the leg ; and, by the large sacrum and ankylosed ilia, for those of the trunk, which is placed almost entirely *in front* of the supporting femora, and always more or less at an angle with them, except in the Grebes and Penguins. The centre of gravity is not, in birds, directly above these supports, as in the true erect position of man, but is placed considerably in advance of the femurs, and necessitates considerable flexion of the lower parts of the legs, and great length of toes, to keep the centre of gravity within the base of support. The long pelvic muscles, the tendons of which reach to the toes, by a constant tendency to flex them, contribute mainly to preserve this semi-erect position, even during sleep, and independently of the will of the animal.

The pelvis of the *Cursores* (*fig.* 106.) approaches most nearly in the massiveness of the bones to the Mammalian type, as well as, in the Ostrich, in the formation of a pubic symphysis.

The *sacrum* (*a*) is very long and narrow, and is composed, according to Cuvier's tables, of twenty pieces in the Ostrich and of nineteen in the Emu and Australian Cassowary. The spinous and transverse processes are distinct, and coalesced only at their ex-

Fig. 106.



Dorsal view of the pelvis of the Ostrich : a, coalesced sacral spines ; *b*, ilium ; *c*, *c'*, sacro-iliac plate ; *d*, sacral chink ; *e*, ischium ; *f*, ischio-sacral buttress ; *g*, pubis ; *h*, symphysis ; *i*, acetabulum ; *k*, anterior ischio-pubic suture ; *l*, anterior obturator opening ; *m*, ilio-pectineal spine ; *o*, posterior or greater obturator hole.

tremities (*a*), in the Ostrich (the former being the only part of the sacrum appearing dorsally), presenting another close approximation to the Mammalian condition.

The *coccyx* is straight, and composed of seven pieces, which are perforated for the termination of the spinal marrow, and end in a conical bone. In the Rhea or American Ostrich, both the sacral and coccygeal bones are much atrophied.

The *ilia* (*b*) are comparatively very short, especially in the Rhea. The alæ are thick, short, and little curved, and lie close to each other at the upper half of their inner borders, by which they are ankylosed to the sacral spines, whose coalesced extremities are seen between them, forming a tent-like eminence above the anterior sacral vertebræ, and supported by their spinous processes in the manner of tent poles. Anteriorly, they overlap the posterior ribs ; and posteriorly, they are prolonged on the sides of the sacrum into a distinct and prominent *ilio-sacral element*.

This is an elongated piece of bone, with a superior (*c*) and a lateral (*c'*) surface, tapering gradually to the posterior extremity of the sacrum, where it terminates in an outward curve; and placed upon the transverse processes, which it encases, like a frame, on each side, and to which it is firmly ankylosed by its inner surface. In the Ostrich, its thick upper surface or border does *not* unite with the similar bone of the opposite side, nor with the sacral crest; but is separated from it by a chink, or oval opening, *d*, gradually narrowing posteriorly, in which the sacral spines (*a*) are seen distinct and separate, and coalesced only at their extremities. Opposite the three last sacral spines, however, the ilio-sacral pieces are ankylosed to the sacral ridge, and terminate posteriorly the oval chink. In the Emu and Rhea, the ilio-sacral pieces are coalesced in their whole length with the extremities of the sacral spines, and a narrow diamond-shaped dorsal plate is formed, composed almost entirely of the united ilio-sacral plates, and having its angles at the massy ischio-sacral buttresses.

The *ischia* (*e*) are very long and thick, and form, by the superior vertical bifurcation of the cotyloid extremity, a very strong *ischio-sacral buttress* (*f*), coalescing at that point with the ilium, sacrum, and ilio-sacral plate. In the Ostrich and Emu the ischia are not connected posteriorly with the sacrum, but a wide and elongated *sacro-sciatic notch* intervenes. In the latter, the ischial extremities are free and tubercular. In the Rhea they are ankylosed, by their posterior four-fifths, not only to the sacrum, but, like the ischia of the Bats, *to each other*, passing in front of the coccyx and greater part of the sacrum, thus excluding them from the pelvic cavity, and enclosing complete *sacro-sciatic foramina*, which open into a sort of posterior pelvic cavity.

The *pubes* (*g*) are long and slender, and are united posteriorly to the ischia in the Ostrich and Rhea, completing the Obturator Foramina; but, in the Cassowary, the pubes, as well as the ischia, are free at their posterior extremities, and the obturator foramina are incomplete, like the sacro-sciatic. In the Rhea and Cassowary they are widely diverging; but in the ostrich they approach each other in a wide curve posteriorly, and unite in a median *interpubic symphysis* (*h*), which curves forward anteriorly in a hook-like process, and completes an oblong anterior pelvic outlet with its longest diameter antero-posterior. The *ilio-pubic* angle is 140° in the Rhea, and 155° in the Ostrich and Cassowary. The ilio-pectineal spines are well marked, especially in the Ostrich (*m*). The *acetabula* (*i*) are perforated, and open partly into the pelvic cavity, and partly upon the sacrum, and are so closely approximated that the bodies of the vertebræ only intervene. Immediately below the acetabula, the ischia and pubes are connected, on each side, by the suture of an ischial apophysis with the pubes (*k*), across the obturator membrane, enclosing a smaller obturator opening (*l*), which transmits the vessels and nerves, and intervenes between the larger obturator opening (*o*) and the acetabulum.

In the *Apteryx* the *ilia* are longer and more concave superiorly, and the *ilio-sacral* prolongation short; and both are separated more distinctly from the opposite ones by the coalesced extremities of the sacral spines, forming an elongated ridge of bone down the middle, and separated from the ilia and ilio-sacral pieces by distinct parallel sutures.

The *ischia*, in this bird, as well as in the fossil gigantic *Dinornis*, or wingless bird of New Holland, are not placed, as in the *Cursores* before mentioned, parallel with the ilia, but form an anteriorly retiring or *reversed ilio-ischial angle* of 140°; and they do not coalesce posteriorly, either with the pubes or the sacrum, but have free truncated extremities, presenting a great general resemblance to the pelvis of the Emu. The *pubes* are parallel to the ischia, and, like them, free and divergent.

In the *Natatores* the pelvis is long and broad, and generally much expanded posteriorly by the divergence of the ischia and large sacro-sciatic ossification, for the attachment of the powerful muscles used in swimming; and the great intercotyloid distance gives to their gait its peculiar waddle (*see fig.* 104.). That of the Loons and Penguins, however, is remarkably contracted, long, and narrow, with little intercotyloid distance.

The usual number of *sacral* vertebræ is fourteen, as in the Swan; the Grebe has thirteen, and the Duck fifteen, and the sea Swallow ten only. The *sacrum* is usually very broad; but in the Penguin and Loon it is unusually narrow, and in the former it is united by ankylosis to the last dorsal vertebra. The *coccyx* is usually composed of eight pieces. The Goose and Pelican have but seven, and the Barnacle Goose nine. In Penguins it is strong, and assists in the support of the body in its usual vertical position. It is usually curved much dorsally, affording a larger posterior pelvic outlet.

The *ilia* are moderately long, and overlap the posterior ribs. In the Penguin they are said, by Wagner, *not* to be ankylosed to the sacrum, but connected only by ligamentous union; thus increasing its loose and waddling gait. The *ischia* are very long, divergent, and largely expanded into a very broad *sacro-sciatic element*, enclosing a small sacro-sciatic foramen. They are prolonged posteriorly into a sort of styliform process in the Auk and Puffin. The *pubes* are very long, slender, and divergent, and are expanded at the extremity, and curved inwards in the Swan, Diver, and Gannett. They do not generally unite with the ischia posteriorly; but, in the Swan, Duck, and Pelican, the obturator foramina are completed by the union of these bones, and are small and elongated.

The *Gallinæ* have large and strong pelves, in correspondence with their powerful legs, used chiefly for progression and scratching up their food.

The *sacrum* is broad, and composed of from ten pieces, as in the Turkey, to fifteen in the Pheasant and common Fowl. The *coccyx* has five pieces in the Pheasant and Turkey, and, in the latter, is said not to be perforated for the spinal chord. In the Peacock there are eight pieces, and the terminal bone is a horizontal oval plate to support the radiating feathers. In the tailless Manx variety of the common Fowl, the coccyx is borted into a single tubercular projection.

The *ilia* and *ilio-sacral ossifications* are broad, and the *ischia* long, divergent, and widely expanded posteriorly into a very broad *sacro-sciatic element*, much hollowed out in the pelvic cavity, and enclosing a large foramen (*see fig.* 105. *l*). This is especially marked in the Crown Pigeon, Bustard, Crested Curassow, and Guan. The *pubes* are long, and generally unite with the ischia to complete an elongated obturator hole (*p*). In the Dove, the pubes and ischia are united in their whole length, and the foramen is obliterated, while in the Crested Guan and Trumpeter it is subdivided into an anterior and posterior portion, as in the Ostrich and Rhea.

In the *Grallatores* the *sacrum* is broad, and composed of from ten to twelve pieces, but in the Oyster Catcher there are fifteen. In the Snipe the transverse processes are more or less separated. The *coccyx* is in seven or eight pieces.

The *ilia* and *ischia* are shorter and broader than in the *Natatores*, the former being placed more parallel to the spine, crossing it at about 165°; and the latter forming an *ilio-ischial angle* of 160°. The inter-cotyloid distance is very great, especially in the gigantic Crane, but in the Stork and Bittern the whole pelvis is smaller and more contracted. The pubes are long, diverging, and parallel to the ischia, especially strong in the *Aptenodytes;* and enclosing often a large obturator foramen by coalescing with the ischia. In the Stork, Ibis, and Flamingo, however, there is no such union.

In the *Scansores*, the *sacrum* of the Parrot is short and very broad, the *ilia* and *ischia* also short and broad, as well as the *ilio-sacral* and *sacro-sciatic* bones, inclosing a small foramen; and the *pubes*, uniting with the ischia in two distinct places, encloses a subdivided obturator foramen. The *coccyx* of the Toucan is long and very flexible.

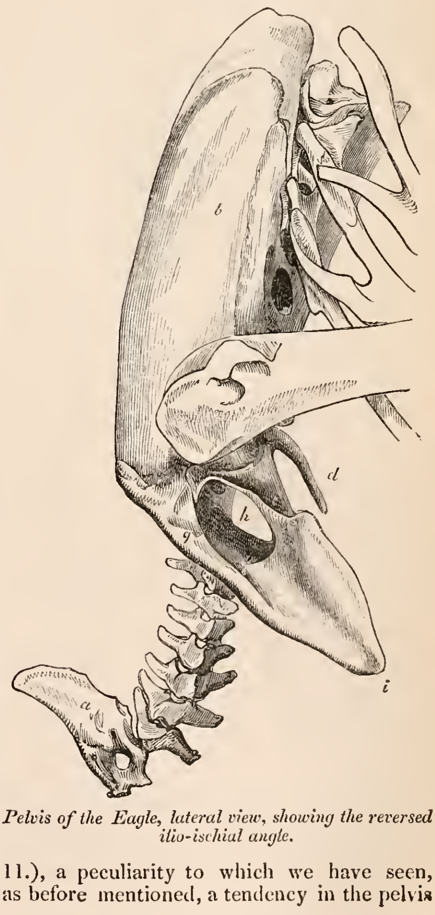
In the *Passeres*, the sacrum is composed of from ten to thirteen pieces; but in the Kingfisher there is but eight. The *coccyx* is in seven to nine pieces, very flexible in the Pies and Swallow; and in the Woodpecker very strong, and supporting on its anterior aspect, near the extremity, a remarkable, round, concave disc, formed by the coalescence and spreading of several of the bones anteriorly. Its use is evidently to support the body by being applied to the stems of the trees to which it clings in the pursuit of its prey and attaching the spreading tail feathers. The *ilia*, *ischia*, and *pubes* are slender in the *Passeres*, and the obturator foramina generally incomplete.

The pelvis of the *Raptores*, or Birds of prey (*fig.* 107.), is narrower, the bones more compact and massy, and less expanded than in the foregoing orders.

The *sacrum* is narrow, and composed generally of eleven bones, which, in the Sparrow-hawk, are ankylosed to the last lumbar vertebra. The *coccyx* is straight, and in seven or eight pieces, with a large and blade-like terminal bone directed dorsally (*a*).

The *ilia* (*b*) are proportionally larger, and project more dorsally than in the other orders, overlapping the spine with elongated wings, concave externally; and a strong tapering *ilio-sacral plate* (*g*), which is directed much downwards, as well as backwards, to unite with the sacro-sciatic plate (*e*) behind the foramen, so as to cross the line of the coccygeal bones almost at a right angle. The *ischia* (*c*) are rather short, strong, and *convergent* posteriorly, where they terminate by a long and pointed spine (*i*), with a strong but narrow *sacro-sciatic ossification* enclosing a small foramen (*h*). The *ischio-sacral* cotyloid buttresses (*f*) are largely developed. The *ilio-ischial angle* is remarkable in being *reversed* or turned forward to a marked extent,—130° in the Eagle, and 145° in the Owl (*see figs.* 107. and 112.

Fig. 107.



Pelvis of the Eagle, lateral view, showing the reversed ilio-ischial angle.

11.), a peculiarity to which we have seen, as before mentioned, a tendency in the pelvis of the Tiger and some *Carnivora*, and which has an evident relation to the increase of leverage for the muscular power of adduction required to grasp their prey, as also has the convergent direction of the ischia just mentioned. The *pubes* (*d*) are long, and are like the ischia, less directed backwards, forming an *ilio-pubic angle* of 125° in the Eagle and 140° in the Owl. They have a great inward convergence in most Vultures and Falcons, and in the Hen Harrier and brown Eagle are closely approximated in the median line and connected by ligaments in a sort of short *symphysis;* generally the ischia and pubes unite posteriorly to enclose a small obturator foramen in the Diurnal birds of prey. In some Falcons and Vultures, however, according to Carus, they are united in their whole extent; while, in the Owls, this union does not take place at all.

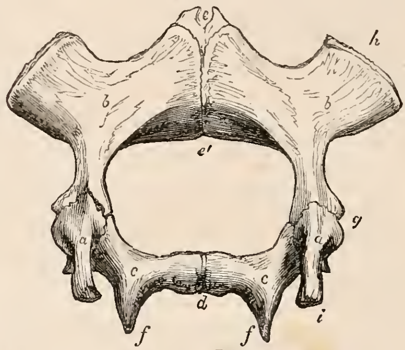
The *Reptile* pelves present some specimens which approach the Mammalian type, in the formation of a perfect pelvic girdle by inter-pubic and inter-ischial symphysis. In these animals, however, the three components of the innominate bones remain separate throughout life, and are connected in the acetabula by ligament only. The manner of articulation of the ilia with the sacrum is also characteristic. We have seen that in Mammals this connection of the ilia takes place about the centre or at the anterior half; and in Birds by the whole length of the alæ. In Reptiles it takes place by the *tip only* of the upper extremity of the ilia, giving much less strength, but far greater mobility to these bones. In the *Chelonian* and *Saurian* reptiles also, the ilia are directed *forwards* and downwards instead of *backwards* and downwards, as in Birds and Mammals, and thus the axis of the anterior pelvic outlet is directed *upwards* and forwards, and the lumbar vertebræ, instead of the coccygeal, form part of the posterior pelvic wall. The pelvic bones are simple, and the sacro-sciatic notch can hardly be said to exist.

In the Ophidians and some Saurians the pelvis, like the corresponding extremities, is totally wanting.

In the *Chelonia*,—the fresh-water, and the mud Tortoise, or *Trionyx*, have a *sacrum* composed of three pieces, soldered, like the dorsal vertebræ, to the back-plate. Their long transverse processes project from it, and unite in a tubercle at their apices, to which the ilia are attached. The *caudal* vertebræ are numerous.

The *ilia* (*fig.* 108. *a.*) are short, thick, curved roundish and clubbed inferiorly, and are directed outwards, forwards, and downwards, extending under the back plate directly between the sacrum (at *i*) and the acetabula. In the Tortoise and Trionyx they are moveable upon the sacrum forwards and backwards. From the acetabula, the *ischia* (*c*), larger than the ilia, pass, almost at a right angle, backwards and inwards, and unite in a *median symphysis* (*d*), forming the real pelvic circle, and presenting a sharp angle posteriorly in the Trionyx (*f*) and fresh-water Turtle. In the land and fresh-water Tortoise this symphysis is continuous anteriorly with the *inter-pubic* (*e*), forming with it a cross-shaped suture, and the obturator foramen on each side is distinct and separate; but, in the Turtle and Trionyx, as in most reptiles, the inter-pubic and inter-ischiatic symphyses are separated and connected by cartilage only, and thus, in the dry bones, the obturator foramina are coalesced in one large opening, and the pubes and ischia have the appearance of large ribs connected at their ventral extremities. The *pubes* (*b*) are the

Fig. 108.



Pelvis of the Trionyx, or Mud Tortoise, superior view.

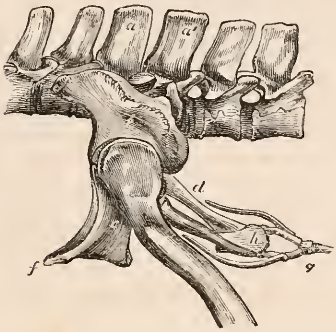
largest of the bones in the reptile pelvis, and, as seen in the Turtle, pass each from the acetabula as a thick bone, which expands as it passes downwards into a broad plate, and divides into an inner portion which unites with its opposite fellow in a *symphysis* (*e*, *e′*) and an outer portion, free and directed externally (*h*). In the *Chelydes* all the pelvic bones are ankylosed to the plastrum or to the back-plate; but in the others, the ischia and pubes are connected to the plastrum by ligaments only. The anterior pelvic opening in the *Chelonia* is directed *upwards* and forwards.

The pelvis of the fossil *Plesiosaurus* is very like that of the Tortoise, with narrow, small, and weak ilia, with the fan-like, spreading ischia, and large square pubes uniting in a common symphysis, by a crucial suture. The pelvic and shoulder bones have a great resemblance in the Chelonian as well as in the Saurian reptiles.

Of the *Saurian* reptiles the Crocodiles have two *sacral* vertebræ with large spines (*fig.* 109. *a*, *a′*), which support the ilia by strong prismatic apophyses, ankylosed together at the ends, and separated by a suture, in the young animals, from the bodies of their vertebræ. The *caudal* bones in all the Saurians, are very numerous.

The *ilia* (*b*) are very short, and in some species almost cuboid, slightly bent, with an inward concavity, and directed downwards and a little forwards, but almost at right angles to the spine, with the superior angle (*c*) projecting backwards. The *ischia* (*c*) are long, and directed, like the sides of an isosceles triangle, downwards and inwards, uniting in a median symphysis (*f*), and much resemble the coracoid bones of the shoulder. The *acetabula* of the crocodile look directly outwards, have strong inter-articular ligaments, and are formed only by the ilia and ischia, the latter presenting, just below the acetabulum, anterior apophyses which support the pubes. The *pubes* (*d*) are directed much forwards, downwards, and towards each other, but do not touch in the median line, being united only by the abdominal aponeu-

Fig. 109.



Pelvis of the Gangetic Crocodile (side view).

rosis (*h*). They are connected by the anterior border with the posterior abdominal ribs (*g*).

The *Lizards* have, like the crocodiles, two sacral bones, as in the Iguana and Great Monitor. In many Lizards the *sacral* transverse processes (*fig*. 110. A, *a*) are very long, and, being articulated by suture to the bodies of the vertebræ, appear, at first sight, like additional ilia. This is particularly the case in a fossil specimen recently discovered by Sir Charles Lyell.* The *ilia* (*b*) are directed forwards and downwards, and the superior extremity projects backwards in a truncated point (*e*). The *ischia* (*c*) are larger, and directed backwards at a great angle with the ilia, uniting in a truncated median symphysis, which is separated from that of the pubes; so that the *obturator foramina* are divided only by ligament (*g*), and communicate in the dry bones. In some Lizards the ischia present posteriorly a spinous projection. The *pubes* participate, with the ilia and ischia, in the formation of the acetabula, present a spine at their cotyloid extremity (*d*), curving downwards and outwards, and unite in a very narrow symphysis; but in the Monitors and Sauve-gardes the pubic symphysis is distinguished by its greater breadth and truncated form (*f*). The *ilio-pubic angle* is about 160°, retiring *posteriorly* in the Great Monitor Lizard, and the *ilio-ischial* angle is very acute, being 60° only (*see fig*. 112. 13.).

In the *Menopoma alleghani* the *sacral* transverse processes are directed backwards, and support apophyses to which the ilia are attached. The *pubes* and *ischia* are short and oblong, and so approximated as to leave no obturator opening.

Upon the pubic spine, in the Cameleon, are two cartilages, which have been stated by Dugès to be of a marsupial character.

Fig. 110.

A, *pelvis of the Great Monitor Lizard.*
B, *ilium, ischio-pubis, and marsupial cartilage of the Salamander (after Dugès), seen from below, and twice the natural size.*

From the pelvis of the fossil *Pterodactyle* Cuvier concludes that the forward direction of the ilia, the anterior position and pointed extremity of the pubis, and the separation of the pubic and ischiatic symphysis, ally this animal to the *Saurian* reptiles.

In the *tailed Batrachia* and *Ichthyic reptiles* there is but one *sacral* vertebra supporting rib-like transverse apophyses which connects them to the ilia. The *ilia* are long and slender, and the *pubes* and *ischia* are blended together in one large, squarish, cartilaginous plate, not perforated, and loosely connected by ligament with the one of the opposite side.

In the *Proteus* the ilia are small, and the whole pelvis very little ossified. In the Salamander, also, the ilia are small (*see fig*. 110. B, *a*). A cartilage, of a Y shape (*d*), is placed at the anterior margin of the ischio-pubic plate (*b*), which Dugès looked upon as marsupial, but which Meckel has considered as part of the sternal elements, and which is a bifurcated prolongation of the cartilaginous ischio-pubic symphysis (*c*). There is also a very small obturator opening in the ischio-pubic plate (*b*). The ossification of the pelvic bones in these animals, according to Dugès, takes place in the same order as in man. The pelvis of the *Axolotl* is, like that of the Salamander, not quite ossified. In the *Siren*, according to Cuvier, there is no vestige of a pelvis. In the *Ophisaurus*, *Cæciliæ*, and *Amphisbæna*, there are only rudimentary vestiges of the ilia and ischia; and in the *apodal Saurians*, as in the *Ophidia*, a single bone only is found, under the skin near the anus. In *Pseudopus anguis* and *Acontia* are simple elongated pelvic bones, articulated by ligament to the last dorsal transverse processes. In *Eryx boa* a pair of elongated bones lie parallel to the rectum, free from the spinal column. They are sometimes found in several distinct pieces.

In the Sauroid reptiles the *acetabula* are directed horizontally outwards, and the inflexions of the feet are made perpendicularly to the rachis or plane of motion, the thigh being

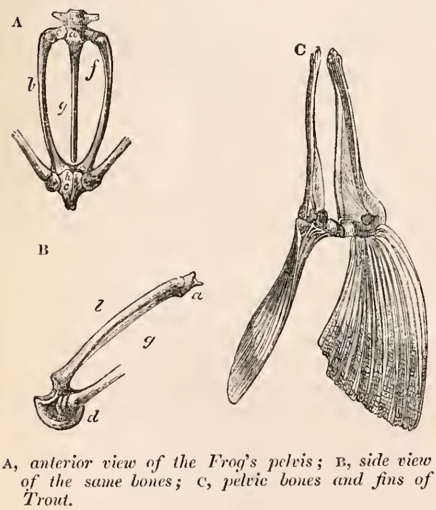
* Lecture at the Royal Institution.

directed outwards, the knee always bent, and the body trailing. They walk on the fore and hinder legs alternately, and leap by a sudden flexion of the body.

The pelvis of the *Anourous Batrachia* is interesting from the changes which affect it, in their transition from the ichthycic to the quadrupedal condition.

The *sacrum* of the Frog (*fig.* 111. A and B) is considered by Dugès to be formed by the last dorsal vertebra, which closely resembles the preceding ones, except in having very long and strong transverse processes (*e*), to the tips of which the ilia are moveably articulated. In the *Rana pipa* and Toad, however, the sacrum presents evident indications of a division into two vertebræ, there being on each side a foramen for nerves, with two prismatic and very rough transverse processes. The *coccyx* of the Frog is composed of two pieces (*f*), which, in the adult state, are ankylosed together and to the sacrum, and considered by some to form part of that bone. They are formed, respectively, from three points of ossification. In addition to these there is a long cylindrical terminal spinous or btyloid process (*g*), which is formed by a single separate ossific point, and becomes ankylosed so the other part at the adult period. This is tonsidered by some to be a second sacrum, end by others a coccyx. It has been supposed ay Dugès to cause, by its progressive ossific development, the mortification and dropping off of the tail at the period of transition from the tadpole condition, and thus closing up the spinal canal posteriorly.

Fig. 111.



A, *anterior view of the Frog's pelvis;* B, *side view of the same bones;* C, *pelvic bones and fins of Trout.*

The *ilia* (*b*) are very long and cylindrical, and directed backwards, becoming almost horizontal in the *Rana pipa*. They suspend between them, by their apices, the long transverse processes and body of the sacrum, like the springs of a coach. At their opposite extremities tney are ankylosed, not only with the ischia and pubes, *but with each other* (*h*) ; and thus the *acetabula*, of which they form the greatest portion, are closely approximated, and the pelvic outlet assumes a V shape with the base at the sacrum and the angle at the coalesced extremities of the ilia. The *pubes* and *ischia* of both sides are coalesced together in an azygos osseous plate (*c*), with a central rounded crest marking the position of the symphysis (*d*), the pubes being the last to ossify. There is no foramen obturatorium. The posterior outlet of the Frog's pelvis looks almost directly upwards, and the anus opens, at the extremity of the coccygeal spine, upon the dorsal aspect of the animal.

In the immature Batrachian a triangular-shaped cartilage intervenes between the opposing ilia and the other pelvic bones in the acetabula, which afterwards becomes obliterated by the ankylosis of the bones. Dugès calls it an "os paracotyleal," analogous to the "paraglenal" bone of the shoulder of the same animal. There are also epiphysial pieces on the ilia and ischia which represent the crest and tuberosity of those bones respectively.

The solidity and firmness of union of the ischio-pubic portion of the pelvis in the frog is a remarkable instance of modification and adaptation of form to meet the requirements for a strong and firm hold for the powerful *triceps cruris*, external obturator, hamstring, and adductor muscles in the thigh of this animal. The single pair of *glutei* also obtain an extensive attachment from the long ilia, and the *pyriformes* from the long coccygeal spine, while the strong abdominal muscles, acting on the moveable ilia, give, as it were, an additional segment to the hinder extremities. In this manner the frog's pelvis is strikingly and directly adapted to its leaping progression.

In the *Fishes* the pelvic structures dwindle to elementary pieces, such as we have mentioned in the bimanal and apodal Reptiles, and finally disappear altogether.

The pelvis is represented in these animals by two bones, sometimes coalesced into an azygos bone, which support the ventral fins. In the *Pisces thoracici* these are suspended by ligament to the coracoids, by which they are advanced anterior to the pectoral fins, and connected to the head; but in the *Pisces abdominales* they are detached from the coracoids, and are suspended in the muscles at the posterior part of the abdomen. They are, however, subject to great diversity of position.

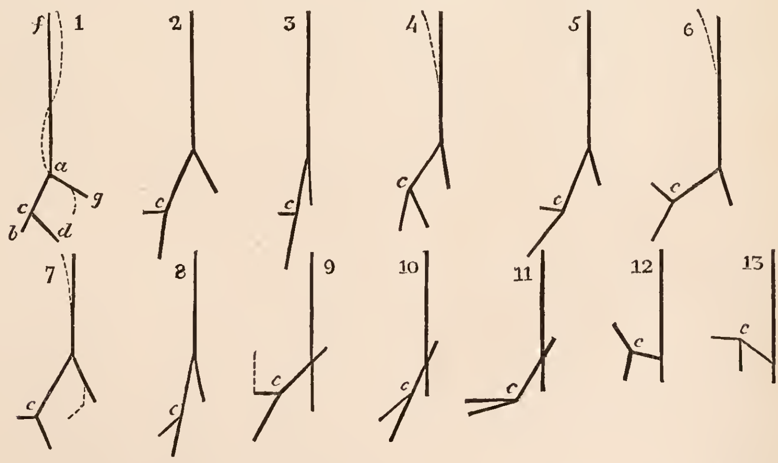
Owen considers the pelvic bones of fishes to be the homologues of the *pubes ;* but, in the opinion of Carus, they are to be considered as *ilia*. Their inferior and ventral position, their occasional union in a symphysis, their frequent coalescence, and their attachment to the generative organs, however, would support rather the conclusion of Professor Owen; the support of the bones of the extremities not being *exclusively* the *iliac* attribute, but also usually contributed to by the pubes and ischia. In Fishes, a supporting arch from the spinal column to the posterior limbs * is not wanted, but rather a free and unimpeded motion for the caudal extremity, used in propelling the body.

In the Angler there are two pelvic bones, each consisting of a vertical portion, which, in this instance, seems to represent the *ilium*, and a horizontal one, which meets in a symphysis with the one on the opposite side, and is the homologue of the pubis, the pectoral rays being attached to the angle of union of the two portions. In the Rays and Sharks, where the pelvic extremities are better developed than in other fishes, the pelvic bones consist of one piece, placed transversely, resembling that which supports the pectoral fins, and suspended loosely, like it, by a ligament to the spine. In the Sharks and *Chimeræ* are found, articulated to it, by means of an intermediate cartilage, two club-shaped bones, called *claspers*, which are used to embrace the female in the generative act. In the *Torpedo*, and also in the *Cyclobates oligodactylus*, an extinct Ray, the pubic bone sends forward two processes, somewhat resembling marsupial bones. In the Sturgeon, the pelvic bones are almost entirely separated from each other, and consist of small triangular pieces, with their apices directed forwards, and supporting the cartilaginous fin rays. In the Cod-fish there are two sub-triangular bifurcated bones, connected to each other by ligament, and suspended from the *coracoids*, the rays of the ventral fins springing directly from them. In the Trout, the pelvic bones are also two in number, flat and of an elongated triangular shape, with the base directed posteriorly, and supporting the ventral fins (see *fig*. 111. c). In the Haddock, there is a single bone, presenting a central oval opening with the shorter diameter transverse. In the *Cyprinus*, *Scomber*, and *Zeus*, they present backward spinous projections. In the *Rhombus* and *Loricaria* there is seen an ankylosis of the anterior caudal vertebræ, forming a sort of *sacrum*, and presenting the first indication of the formation of this bone in the animal kingdom.

Subjoined is a table, showing the comparative pelvic angles in Man and the principal genera of Mammalia, Birds, and Reptiles. The measurements were principally taken, with great care to insure correctness, from the specimens in the Hunterian Museum, through the kindness of Professor Owen. The relative size or total disappearance of the *vertebro-iliac*, *sacro-vertebral*, and the *ilio-pubic* and *ilio-ischial angles* in the different tribes, will be here seen at one view. It may be observed that the two former may vary somewhat through inaccuracies in articulating the skeleton, or with the variations of the vertebral curve, and that the results here given are to be taken in this particular, as approximative only. But the ilio-pubic and ischial angles cannot, from the ossific union of the bones, be subject to such accidental variations.

The accompanying diagram is intended to show the absolute lines of direction or axes of the pelvic bones and spine seen in profile, with the angles above referred to, in the principal pelvic types.

Fig. 112.



Lines of direction and profile angles of the pelvic bones. 1. Human type; *fac*, vertebro-iliac angle; *fag*, sacro-vertebral angle; *acd*, ilio-ischial angle; *acb*, ilio-pubic line, forming *an angle* in all other animals. 2. Orang type. 3. Monkey type, *no* ilio-ischial angle. 4. Edentata type, ilio-pubic angle *reversed*. 5. Carnivora type, ilio-ischial angle *reversed*. 6. Pachyderm type. 7. Ruminant type. 8. Rodent type, *no* ilio-ischial angle. 9. Kangaroo type. 10. Bird type, *no* ilio-ischial angle. 11. Raptores type, ilio-ischial angle *reversed*. 12. Chelonian type. 13. Saurian type, ilio-pubic angle *reversed*, and remarkably *acute* ilio-ischial angle.

TABLE OF COMPARATIVE PELVIC ANGLES.

	Vertebro-iliac.	Ilio-pubic.	Ilio-ischial.	Sacro-vertebral.
	Degrees.	Degrees.	Degrees.	Deg.
1. Man - - -	155	0	110	117
2. Orang - - -	160	125	165	150
3. Chimpanzee - -	155	120	do.	160
4. Gibbon - - -	do.	130	0	170
5. Baboon (brown) -	do.	110	0	155
6. Monkeys - - -	160 to 170	90 to 120	0	0
7. Lemur (albifrons) -	170	120	0	0
8. Loris gracilis - -	do.	75	0	0
9. Sloth (Ai) - -	145	155	135	0
10. Mylodon (fossil) -	125	155 *reversed*	120	160
11. Megatherium (ditto)	—	do. *reversed*	125	—
12. Armadillo - -	155	150	145	0
13. Ant-eaters - -	140	155 *reversed*	do.	0
14. Lion - - -	150	120	0	170
15. Tiger - - -	160	110	165 *reversed*	do.
16. Leopard - - -	150	120	0	do.
17. Hyæna - - -	140	125	0	160
18. Bear (brown) - -	do.	do.	0	do.
19. Badger - - -	do.	130	0	170
20. Racoon - - -	150	145	160	0
21. Elephant - - -	120	100	145	170
22. Rhinoceros - -	125	150	do.	do.
23. Hippopotamus -	160	125	170	160
24. Hog - - -	145	120	do.	do.
25. Tapir - - -	125	145	140	0
26. Horse - - -	130	130	145	0
27. Ox tribe - - -	145 to 150	130	130	150
28. Deer tribe - -	150	140	150	160
29. Irish deer (fossil) -	145	135	do.	do.
30. Giraffe - - -	150	140	145	170
31. Camel - - -	140	120	155	155
32. Sheep and goats -	145	130	150	170
33. Rats and mice -	170	150	0	0
34. Hare - - -	165	120	0	160
35. Jerboa - - -	140	145	0	0
36. Kangaroo - -	do.	135	170	0
37. Wombat - - -	160	130	do.	0
38. Thylacinus (cynoceph) - - -	150	115	do.	0
39. Ornithorhyncus -	140	120	155	0
40. Echidna (hystrix) -	do.	110	0	0
41. Hedgehog - -	130	150	0	0
42. Bat (Ternate) -	0	100	0	0
43. Birds, generally -	150 to 160	155 to 160	0	0
44. Ostrich - - -	160	155	0	0
45. Rhea - - -	do.	140	0	0
46. Cassowary - -	do.	155	0	0
47. Apteryx - - -	155	140	140 *reversed*	0
48. Eagle - - -	150	125	130 *reversed*	0
49. Owl - - -	do.	140	145 *reversed*	0
50. Chelonian reptiles -	80 to 100	130	80	0
51. Crocodiles - -	60 to 90	140	130	0
52. Lizards (Monitor) -	40 to 90	160 *reversed*	60	0

Having thus taken a general review of the progressive development of the pelvis, and traced it from its most perfect form in man to its most rudimentary elements in the fishes; we can enter more prepared into the consideration of the *serial homologies* of the pelvis and its ligaments.

SERIAL HOMOLOGIES OF THE PELVIC BONES AND LIGAMENTS.

The *sacrum*, according to Professor Owen, is to be considered as the *centrum* of the pelvic vertebral elements. The ankylosed bodies of the sacral vertebræ, as well as their coalesced laminæ, spinous and articular processes, are sufficiently evident as the representatives of those components of the neural arch in the typical vertebra.* The lateral masses of the sacrum which support the ilia are, however, made up of two elements coalesced together, as is shown in the manner of their development, before described, viz., *first*, of the true transverse processes, or "*diapophyses*," constituting the external row of tubercles seen on the *posterior* surface of the sacrum, and which are ossified, like those of the true vertebræ, by extension from the same points of ossification as the laminæ, and spinous and articular processes; and, *secondly*, of the six *characteristic* sacral ossific points, three on each side of the three upper sacral bodies, which are placed on the *anterior* surface of and below the former, between the sacral foramina, as before described.

These ossific points, as shown in preparations exhibited to the British Association, in 1837, by Mr. Carlyle, were four in number on each side, and very distinct from the true transverse processes; and they were considered by him to represent the necks and heads of four *sacral ribs* on each side. Upon the truncated extremities of these three or four sacral ribs the *auricular facets* are supported. They appear to be similar to the anterior roots of the cervical transverse processes, upon the last of which is occasionally developed, in the human subject, a short costal process. In the nomenclature of Professor Owen, they may be considered the sacral "*parapophyses*," but differ from these processes as seen in the rib-bearing vertebræ of the Crocodile, in being developed by separate and distinct centres. Blainville remarks that the four upper sacral vertebræ, scientifically considered, compose the whole of the true sacral elements; and that the fifth, which he calls "*subsacral*," is an ankylosed coccygeal vertebra. But the lateral epiphysial plates of bone before described — the upper of which forms the auricular facet, opposite the three first, and the lower, the sides of the two last sacral vertebræ — would seem to connect these vertebræ more particularly together, and to be the coalesced serial homologues of the epiphyses forming the articular facets on the *tubercles* of the ribs. In the Saurian reptiles these sacral ribs, two in number on each side, are very distinctly analysed, and have been before mentioned as intervening between the sacrum and the ilia. The anterior of these ribs in the Saurians are said by Mr. Carlyle, to be articulated to the bodies of the last dorsal and first sacral vertebræ, as well as to the intervertebral substance between them; and the posterior, to the last sacral and first caudal vertebræ, and to their intervertebral substance — affording an exact homologue to the true ribs. The ilia in the human fœtus, and for some years after birth, are connected to two only of the sacral vertebræ; but, in the adult state, they

* A remarkable analogous instance of the coalescence of vertebræ to form one solid mass is seen in those of the cervical region of the bottle-nosed Whale.

join three sacral ribs, corresponding, as we have seen, to the three upper sacral vertebræ. Mr. Carlyle has seen them, in the negro, join four sacral ribs, as above stated.

The *sacral element* of the pelvis we have found to be most largely developed in Man, and its angle with the spinal column most marked, in adaptation to his destiny for the erect and bipedal posture. In Birds, also, of bipedal and semi-erect position of body, it is also large, and, in a less degree, in animals whose climbing or sedentary habits require an habitual upright direction of the vertebral column, such as the Apes, Bears, and Sloths; while it is much contracted, both in breadth and length, in most of the animals of true quadrupedal progression. Its spinous processes are long, and sometimes united in a crest, in the springing animals, and those requiring long leverage for the muscles of the back and thigh arising therefrom.

The *coccygeal* pieces are, in the human subject and the higher *Simiæ*, the aborted continuations of the sacral vertebræ, gradually diminishing into their most permanent and principal elements,—the bodies of the vertebræ. The upper ones show also rudimentary transverse processes, and the first presents well marked articular processes to join with those of the sacrum, or sacral horns. Dr. Knox considers the 1st coccygeal vertebra to be the representative, in man, of a class of vertebræ distinct both from the sacral and remaining coccygeal.

In Man these bones are placed very obliquely, to support the pelvic viscera; but in the lower mammals, the Birds, and especially the Reptiles and Fishes, they are placed in the line of the vertebral column, and are developed as caudal vertebræ, in adaptation for their various uses in propulsion or prehension, &c. In many, they present not only a complete neural arch and spine, enclosing the caudal continuation of the spinal chord, but also an anterior or hœmal arch and spine, to enclose and protect the arteries of the tail.

The *ilia* evidently consist of the shafts of the three or four sacral *ribs*, coalesced into one mass of bone on each side, and constitute the homologues of the shafts of the thoracic ribs, termed by Owen the "*pleurapophyses*." The descending branch or body of the ischium is considered by the same writer also to form one of these pleurapophyses. The development of the whole of the *ischium*, as well as the *pubis*, from a single and separate centre; and the connection of both these bones to the ilium in the cotyloid cavity, seems, however, to place the whole of each bone in the same relative position, and to class them both with the chondro-sternal elements, or "*hæmapophyses*" of the thoracic ribs. Professor Owen considers that the pubes and the ascending rami only of the ischia are the homologues of the rib cartilages,—an arrangement that would make a separation of the ischium, which its mode of development from a single centre would hardly justify. The bent and hook-like form of the Mammalian ischia finds a very close counterpart in the *cartilages* of the eighth ribs, in Man, especially when these are ossified, as often occurs; and the manner of its junction with the pubes in the human subject is exactly similar to that of the eighth cartilage with the seventh, before it reached the sternum. In many of the lower Mammalia, especially in the Marsupials and in the Reptiles, we have seen that the ischial ribs reach each other, and are connected, like the pubic, in the median line. The formation of a pubic apophysis or descending ramus to meet the ascending ischium, is a disposition which finds a counterpart in a similar apophysis from the acetabular end of the ischium to support the pubes, which we have seen in the pelvis of the Crocodiles, excluding the latter bone from participating in the formation of the acetabulum, exactly as the ischia in man and some animals are excluded from the formation of the median symphysis. The greatest extent of this ischio-pubic coalescence is seen in the Batrachians and the saltatory *Carnivora*, Ruminants, and Marsupials; its entire absence in some of the Chelonian and in the Saurian reptiles. In the Birds and Bats it is often present even where there is no median symphysis.

The *iliac element* has been seen to be largely developed in its shaft, and placed very obliquely on the lumbar vertebræ in quadrupeds characterised chiefly by saltatory quadrupedal progression, and requiring long hold for the great muscles of the hip, as the *Carnivora*, the Deer tribe, the Monkeys, the Horse, and the Frog,—while it is contracted to a remarkable degree in the Walrus and Seal, which approach in their habits the Cetaceans and Fishes, in whom the iliac element of the pelvis is the first to disappear altogether. Its alæ we see *elongated* behind the sacrum in those animals whose pseudo-sedentary habits require a long leverage for the muscles of the back arising from the iliac crest, such as some of the *Rodentia* and the Kangaroos—and its alæ, on the contrary, to be *expanded* in those requiring support to the abdominal viscera, either from their size, as in the *Pachydermata*, or from the erect or semierect position, as in Man and the Sloths.

The *ischiadic element* has been seen to be adapted—by its large development and direct line with the ilia, for saltatory progression, requiring a long leverage for the flexor muscles of the leg, as in the *Carnivora*, the Deer tribe, the Rodents, the Kangaroos, and the Birds;—or, for the support of the sacrum, by its angularity with the ilium, and by its elongated tuberosities, in the Ox, Hippopotamus, and some others, and by ankylosis with the sacrum, as in the Sloths, Bats, and Birds;—or for the support of a carapace, as in the Armadilloes;—or for the true ischial sedentary support of the body, as in the Apes and Monkeys.

The *pubic element* has been likewise seen to be in a direct line with the iliac shaft in Man *only*, destined to the truly erect posture;—and in those animals formed for quadrupedal progression to be short and placed at a more or less marked ilio-pubic angle, so as to be out of the way of the approximated femurs, in their semi-flexed and angular movements on the pelvis;—but in those habitually requiring a semi-erect position, as the Sloths, to be longer and less angular. It is also unusually long and oblique in the Seal tribe, with reference, probably, to a tapering extremity and fish-like outline.

The *iliac crest* and its *posterior spines* and *tuberosity* are the hypertrophied, coalesced, and spread-out *tubercles* of the sacral ribs, a homologue which will be made more evident by the consideration of the homologues of the pelvic ligaments. The epipleural spines of Fishes, and the costal appendages of Birds, show the serial homology of these processes.

The *Y-shaped epiphysial cotyloid bone* of M Serres has been considered by some to represent a marsupial bone; but, seeing that in the marsupials themselves these Y-shaped bones and the real marsupial bones also, coexist, this opinion cannot be considered as tenable.

In the immature Potoroo, as described by Owen, there is another epiphysial cotyloid bone forming part of the anterior margin of the acetabulum (see *fig.* 110. Art. *Marsupialia*); and one of a similar nature and position is described by Geoffroy St. Hilaire as present in the acetabula of the Rabbit, and is considered by him to be a rudimental marsupial bone. There seems, however, greater reason to suppose that both these cotyloid epiphyses are rather of the nature of those *complementary* ossific points which are seen in the opposed articular surfaces of the bodies of the true vertebræ, and also in the sacral vertebræ, and in the articular ends of some long bones,—as those forming the elbow-joint.

From the position of the *ilio-pectineal eminence* or *spine* at the junction of the ilium and pubes opposite to the superior limb of the cotyloid Y-shaped bone, it would seem as if this process were connected with it by a continuation of its ossification upwards. As this spine is coexistent, as seen particularly in the Monotremes, in a great state of development with the marsupial bone, the opinion that it represents that bone, seems to be quite untenable. We have seen it most developed in those animals whose posture or structure requires largely-developed *psoæ parvæ* muscles, as in the Marsupials and Monotremes; the tendons of those muscles being implanted upon them, presenting a close similarity to the implantation of the *anterior scaleni* muscles into the *scalene tubercle* of the first rib, to which this eminence would be thus homologically related.

The *marsupial bones*, being developed in the tendons of the external oblique muscle, present the greatest homology, both in position and office, with the *spines* of the *pubes* in Man and some animals; and it would appear, from the manner in which the cremaster muscles play over them, as if they were formed by an ossification of that part of the tendon which is called, in human anatomy, the *external pillar* of the ring, or *Poupart's ligament*, and which is implanted upon the pubic spine.* In support of this opinion, it may be stated that, in Poupart's ligament near the spine of the pubis, *cornicles*, similar to those in the stylo-hyoid ligament, are said to have been found in the human subject. The cartilages upon the pubic plate of the Cameleon, before mentioned, are also significantly homologous to these cornicles and to the marsupial bones, as well as that upon the anterior pubic angle in the Salamander, and considered by Dugès as having a marsupial character.

The *epiphysial plates*, forming the articular surfaces of the pubic symphysis in man, are analogous with those which form the *auricular sacral* facets.

In the immature Potoroo, there is a triangular wedge of bone inserted, with its apex forwards, between the pubic bones posteriorly; and, in the adult Kangaroo, we have seen that a single V-shaped epiphysis is placed with the apex upwards, between the ischial bones at the lower part of the ischio-pubic symphysis, and forming a prominent vertical median ridge on its anterior aspect (see *fig.* 99. *c*). These epiphyses appear to result from ossification, by independent centres, of the inter-pubic and inter-ischial fibro-cartilages, and to constitute, in these animals, a serial homology with the *central ossific points* of the *sternum* and *xiphoid appendix*; and they may be considered as represented in the human subject by the *inter-pubic fibro-cartilages*, which are continued along the abdominal walls to their sternal homologues by the *linea alba*; as the pubic and ischial elements themselves are represented by the *lineæ transversæ*, and their cotyloid junction by the external border of the *aponeurosis* of the *external oblique muscle* and the *linea semilunaris*. The *two cartilaginous plates* of the pubic symphysis would seem to be the homological representatives of the *double lateral ossific points*, often found permanently separated by an opening in the lower pieces of the human sternum, and in the bifurcated xiphoid appendage.

We have seen that, while in the Kangaroos and the leaping Rodents, Ruminants, and Carnivora, the *ischial* and *pubic symphyses* are largely developed and coalesced, and seem, in many cases, to be compensatory for the weakness of the sacral portion of the pelvis; in the Sloths and some others the ischial symphysis is entirely wanting; and in the Bats, Shrews, Moles, and Birds, the elements of the pubic symphysis also entirely fail. A congenital and similar deficiency of this symphysis has been observed in some human pelvic malformations, from arrest of development. This deficiency may be well compared to a like congenital absence of the sternum, some instances of which have been recorded.

The loss of pelvic firmness consequent upon this is compensated for, in great part, in the animals just named, by the ossification of another pelvic element, the *sacro-sciatic*.

* Laurent and Owen consider these bones as sesamoid trochlear ossicles. (See Art. *Marsupialia.*)

These are represented in Man and Mammalia generally by the *sacro-sciatic ligaments*, and appear to be ossified by extension from the epiphysis of the ischiadic tuberosity, and from the ischiadic spine. In Birds, they constitute an important element of the pelvis, and are separated, more or less, from the ischium and sacrum by a faintly marked suture, more evident, however, at the sacral extremity. Taken in a scientific point of view they represent two additional pelvic *rib shafts*, or *pleurapophyses*, of the *two last sacral* vertebræ, and are implanted on the sacrum, in the human pelvis, in the site of the two lower lateral epiphysial plates of that bone, exactly as the ilia are articulated upon the three upper. Their extension to the coccyx would also seem to connect them with the elements of the first coccygeal vertebræ; — and their attachment to the ischia would be, in this point of view, a repetition of the kind of union of the latter bones with the descending pubic rami, as the cartilages of the false ribs are connected consecutively to each other in the thorax.

The *obturator* and *sacro-sciatic foramina*, considered in this light, constitute simply consecutive and enlarged *interchondral* and *intercostal spaces* respectively; the lesser sacro-sciatic foramen becoming, in the Sloths, Bats, and Birds, entirely obliterated. This manner of viewing them explains the apparently indifferent way in which the boundaries of these openings, especially the obturator, are left incompleted, or entirely obliterated, in Birds and Reptiles. The *cotyloid notch* may be thus considered as the commencement of the obturator separation, and the formation of two obturator openings, as in the Ostrich, may be readily explained.

The *obturator membrane* may also be thus related to the *anterior intercostal aponeuroses*, and the *membranous expansion* of the upper border of the *great sciatic ligaments* (before mentioned as connected with the fasciæ covering the internal obturator and pyriformes muscles), to the *posterior intercostal ligaments*.

The homologues of the *ligaments* of the *sacro-iliac* articulations are readily found in those connecting the head, neck, and tubercles of the thoracic ribs to the vertebræ.

The *anterior* and *superior sacro-iliac ligaments* are evidently repetitions of the *anterior* or *stellate costo-vertebral*; the superficial fibres of the *posterior sacro-iliac*, repetitions of the *posterior costo-transverse*; the deep fibres, or *interosseous sacro-iliac*, of the *middle* or *interosseous costo-transverse*; and the *ilio-lumbar* and *lumbo-sacral* ligaments, of the *oblique* or *anterior costo-transverse* ligaments of the ribs. The connection of the last-named ligament with the transverse process of the vertebra above, and with the iliac crest below, is very similar to the oblique direction and attachments of the homologous costo-transverse. The ossification of these ligaments in Sloths, Bats, and especially in Birds, gives additional support to their otherwise feebly connected pelves.

The *ligaments* of the *pubic symphysis* find easily their homologues in the *chondro-sternal* ligaments. The *anterior* and *posterior peripheral inter-pubic ligaments* are repetitions of the similarly placed and constituted *chondro-sternal*, which, like them, connect the hæmapophyses together across the interposed elements, as well as directly to the endo-sternal bones and inter-pubic fibro-cartilage. The *superior pubic* ligament finds its homologue in the *inter-clavicular*, and the *sub-pubic*, in the *chondro-xiphoid* and *interchondral* fibres.

It would be easy also to point out the *muscular* homologues of the two regions; but space will not permit more than to mention the evident ones of the *external* and *internal oblique* muscles with the similarly placed and directed *intercostals*; of the *levator ani* with the *diaphragm*; and of the *pyriformes* with the *psoæ* muscles. The *internal obturator muscles* would represent the *triangularis sterni* and *transversalis abdominis*; and the *external*, the *lesser pectoral* and *external oblique muscles*.

The homologues of the *pelvic* bones with those of the *shoulder* are best seen in the Reptiles. According to Dugès, the pelvis of the Salamander has a close resemblance to the shoulder of the Cameleon.

The *ilium* is generally considered to be the homologue of the *scapula*; the *pubis*, of the *clavicle*; and the *ischium*, of the *coracoid bone*. Meckel considers the body of the *ischium* to represent the spine of the *scapula*; while, in the opinion of Oken, the *pubis* represents the *acromion process*, and the *marsupial bones* the *clavicles*.

In the shoulder of the Cameleon, the scapula is longer even than the ilium, and the furcular clavicles and coracoids are ankylosed together like the ischium and pubis. And, in the pelvis of the Crocodile, we have seen that the ischium excludes the pubis from the formation of the acetabulum by an apophysis which overhangs that cavity, somewhat as the human coracoid process intervenes between the glenoid cavity and the clavicle.

The *ascending branch of the ischium* may, further, be taken to represent the *epicoracoid bones* of the Monotremes, Lizards, Batrachians, and some Fishes, as the Cod, Carp, and Perch, In the Cock-fish, Snipe-fish, and Lancet-fish, these bones are joined in a kind of symphysis, forming an independent arch behind the scapular arch.

And those bones of the scapular arch of the Fish, which are considered by Owen to be the *coracoids*, (but by Meckel, Agassiz, Geoffroy, and Spix to be *clavicles*,) unite also in a median symphysis, presenting an homologous affinity to the *ischial symphysis* seen in the Reptiles,—the whole of these symphysial elements being represented, combined, by the elongated *ischio-pubic symphysis* in many Mammalians, but especially in that of the Marsupials and Monotremes.

(*John Wood.*)

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Pelvis, Abnormal Anatomy of the. — From the close relation of this structure to the processes of child-bearing, the most important of the alterations to which it is liable by disease, are such as produce *deformity* and *obstruction* of the passages, and occurring in the female subject. In the experience of Dr. Robert Lee, about one-sixth of all the cases of difficult parturition in London, depend upon contraction of the pelvis from arrest of development or distortion. In the male subject, they are interesting mainly as to the light they may throw upon the processes and mechanisms of the abnormal changes.

On reviewing a good collection of abnormal pelves, we find them susceptible of the following classification, of which the principal part are interesting chiefly to the obstetrician, but, in a great degree, to the surgeon and general pathologist also.

Pelvic Deformities and Obstructions. — *Deformities* of the pelvis, properly so called, are all such departures from the adult "*standard*," in size, build, and conformation, as are sufficiently *marked* to influence child-bearing.

They have been variously arranged, but seem to fall best under two heads: viz.— 1. *Normal irregularities*—including all those which present the shape and proportions proper to the healthy pelvis at some period of its development; and,—2. *Distortions*,—including all such peculiar alterations of shape and size as are consequent upon disease or injury.

1. *Normal irregularities* may be subdivided into,—*Equable deviations*, in which the general form and appearance are similar, and the diameters *proportionate* to those of the "*standard*" pelvis; and,—*Irregularities from imperfect development*, in which the shape deviates from, and the diameters are *not* in proportion to, those of the "*standard*."

Equable deviations.—"*Pelvis equabiliter justo major.*"—The irregularity in this pelvis consists in all the diameters being in *excess*. It is not uncommon. Burns records one example. Dr. Murphy has another in his possession, and there is in the Museum of King's College a third, the brim of which measures 6 inches transversely, by 5 inches antero-posteriorly. The largest hitherto recorded is one by Giles de la Tournette, who gives

	in.
The distance between iliac crests -	$12\frac{1}{2}$
„ Antero-posterior diam. of *brim* -	$5\frac{1}{2}$
„ Transverse diam. of do. -	$6\frac{1}{2}$
Both the diameters of the *inferior outlet* -	$5\frac{1}{2}$

The *disadvantages* of this pelvis are said to be prolapse and displacement of the viscera, sudden expulsion of the fœtus, inversion of the uterus, and want of the proper impress of rotation on the head. Retroversion of the uterus and its prolapse in the impregnated state, are said by some to be most commonly observed in large pelves.

"*Pelvis equabiliter justo minor.*"— In this pelvis, all the diameters are proportionately *diminished*. The diminution is said, by Churchill, to be generally about one-fourth. Naegele thinks it to be more common than had been supposed by Bandelocque and other writers on midwifery. Velpean gives two cases of "*Etroitesse absolue*" (*Journal Complementaire*), in which the diminution was so great that one woman died undelivered, and the other underwent the Cæsarian operation.

It was considered by Alexander Shaw *, that proportionable contraction of the pelvic diameters is very common in rickety subjects, from want of proper osseous development, and that it is generally accompanied by corresponding diminution of the size of the bones of the lower extremities. The experience of Rokitansky also favours the opinion that this proportionate contraction, without distortion of the pelvis, may be produced by rickets. Naegele, however, records three female pelves affected with this deformity, which presented no appearance whatever of rickety change, neither in strength, weight, nor texture, one being even heavier than usual; nor were there any rickety symptoms in their history. Two of the subjects died after severe instrumental labour; and the third, after one miscarriage, died undelivered of the second conception, from rupture of the uterus; comparison with the child's head afterwards showing, that delivery of a *living* child would have been impossible without the Cæsarian section. The diameters were generally above an *inch* less than the standard measurement. The ages of these subjects were from twenty-three to thirty-two years, showing that the contraction was an adult deformity. They were also about or above the average height. Women of low stature, indeed, have most commonly large pelves as well as large heads, and are not more liable to this deformity than those

* Med. Chirurg. Transactions, vol. xvii.

of taller stature ; the height of the individual being dependent, chiefly, upon the length of the lower extremity and spinal column, which in these cases are disproportionate.

The pelvis of the true dwarf, however, in common with, and in proportion to, the osseous system generally, is contracted and stunted in growth. In the Museum of the Edinburgh Infirmary, is the skeleton of a male adult dwarf, in which the pelvic pieces and epiphyses are not united by bone, but there is no distortion. The jaws are infantile. The pelvic bones in the well-known skeleton of the female dwarf in the Hunterian Museum are in a similar incomplete condition. Sudden and universal "*arrest of development*," is apparently the cause of this curious immature condition.

In Naegele's collection is the pelvis of a female dwarf, aged thirty-one years, whose height was 3 feet 6 inches, the measurements of which are given as a specimen of a distinct kind of "*pelvis equabiliter justo minor*" by that eminent author in the Appendix to his valuable work—" *Das schräg verengte Becken*," as follow —

		in.	line.*
Between the sacral promont. and tip of coccyx	- - - -	3	3
Between the sciatic tuberosity and iliac crest	- - - -	5	5
Between sciatic tuberosity and linea innom.	- - - -	2	7
Superior opening, conjugate diam.	-	3	0
" " transverse do.	-	3	7
Cavity antero-postr. do.	-	3	3½
" transverse do.	-	3	0
Inferior opening, transverse diam.	-	3	0
Length of pubic symphysis	- -	0	11

The pelvis was perfectly regular and normal in symmetry and proportion, presenting all the appearances, in these respects, of the adult "*standard*." The sub-pubic arch, the sacral curves, the direction of the ischia and the curvature of the pectineal line were perfectly regular. The sacral bones, however, and the three pieces of the innominate bones, were united by cartilage only, ossification not having taken place. In this respect only is this pelvis allied to the class of deformities resulting from imperfect development, or to an *immature* pelvis. These peculiarities may possibly be explained by supposing the "*arrest of development*," which dwarfed the woman, to have taken place *after* the age of puberty, and the development of the sexual organs, but *before* the union of the sacral and innominate pieces, that is, between the fourteenth and sixteenth years. This supposition is moreover strengthened by the fact, that the ischio-pubic rami were firmly united, that the woman had menstruated at the proper period, and that all the limbs were in normal proportion to the body. Neither in the history of the case, nor in the appearance of the skeleton, was there any sign of rickets. The woman had become pregnant, and by the advice of the medical attendants, premature labour was induced at the sixth month, and the patient was safely delivered by the forceps, but died ten days afterwards from the consequences of indiscretion in diet.

* Rhineland.

Out of the three cases of *pelvis equabiliter justo minor* given by Professor Busch *, and quoted by Dr. Rigby, there was a fatal termination in two instances. In one case, the pelvic diameters were universally half an inch below the standard size. In another, which resembled that of a child, they were contracted in every direction three quarters of an inch. The last ought, probably, to come under the denomination of an infantile pelvis.

In the above cases, the contraction of the pelvic diameters is marked and *absolute ;* but there is a considerable class of cases, included among the *variations* of measurement of normal pelves, in which the diameters are diminished in a much less degree, and yet their *relative* disproportion to those of a bulky fœtal head may be so great as to call for instrumental aid in parturition. Naegele, however, concludes that the contraction of the pelvis itself (without any complication with unusual bulk of fœtus) should be considered, in most cases, as the cause of the difficulty of labour, and that this kind of faulty pelvis merits the especial attention of the accoucheur as much as others, and the more, that from the absence of evident external symptoms, the difficulty of diagnosis is greater than in rickets or malacosteon.

The *cause* of most of the cases of proportionably contracted and enlarged pelves is only to be looked for among those of Nature's aberrations which result in heads, extremities, &c. disproportionate to the rest of the body. The small pelvis may be considered as one in which the development in *shape* has gone on to completion, but the development in *size* arrested by some cause. This cause has been attributed by Mr. Shaw † to a general rickety disease in many cases.

In addition to its effect in seriously impeding the passage of the fœtal head, a small pelvis of this kind is said by Ramsbotham to cause retroversion of the uterus in some cases.

Irregularities from imperfect development. Infantile pelvis —This form of pelvis is characterised by the persistence of the form of the pelvis which is normally but transitorily present under the age of puberty. Its appearance corresponds, in some degree, with the characters of the infantile pelvis described in the first section of this article, of which, in the respect under consideration, the most important are, the preponderance of the *antero-posterior* diameters, which are *larger* than the *transverse* ; the contraction of the sub-pubic arch ; the shallow and diminished cavity ; the approximation of the ischial tuberosities ; the flat, expanded, shallow, and rounded ilia, and the increased obliquity of the superior plane. The pieces of the sacrum and innominate bones are generally incompletely united by ossification.

In a pelvis described by Naegele ‡, taken from an idiot girl aged twenty-one years, who

* Neue Zeitschrift für Geburtskunde, t. xv. 1837.
† Op. cit. ‡ Op. cit.

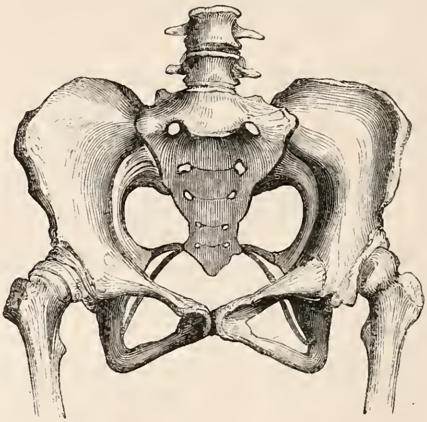
was only 4 feet high, and had never walked nor menstruated, the sacrum and innominate bones were connected by cartilage only, but the ischio-pubic rami were united. It presented, in size as well as form, the characteristics of that of a child of six or seven years old. The conjugate diameter was larger than the transverse, the ilio-pectineal line little curved, and the cavity funnel-shaped, the sub-pubic angle being only 30½°. The bones were not rickety. The organs of generation, both internal and external, were infantile. The measurements and appearance of this pelvis are contrasted by that author with those of the dwarf previously described. The arrest of development seems to have taken place in the present case at a period long before the changes of puberty, as shown by the undeveloped genital organs; so that the cases differ only in the *degree* of immaturity. Such cases as the latter are not likely to require the aid of the accoucheur.

In accouchements at a premature age, however, some of the yet-remaining peculiarities of the infantile pelvis may present difficulties in parturition, among which the contraction of the diameters, if not their want of adult proportions, will be the chief. At the period of puberty, the transverse and oblique diameters enlarge much more rapidly, in the female, than the antero-posterior, and begin to preponderate over them, while, at the same time, and in a great measure in consequence, the pelvis begins to assume its adult "*standard*" appearances. The full development of *size*, however, is somewhat later in being accomplished, and depends upon the completion of the ossification. These changes of the pelvis take place, as explained by Mr. Shaw *, somewhat later than those of the upper parts of the body, in the transition from the infant to the adult state, but proceed to a greater extent, so as to reverse the excess in proportionate size from the upper to the lower extremities. The pelvic growth and the developments of puberty may, according to the same authority, be retarded to a later period than the usual age, fourteen years, by a weakly constitution or rickets; and the female, adult in age, still remains infantile in pelvic development. In a case mentioned by De Fremery †, the three parts of the innominate bone were distinctly separate in a female at so late an age as seventeen years. Some remarkable cases of extreme mobility of the pelvic bones in children are also related by Deventer.

But the development in *size* may proceed to its fullest extent, and yet the development in *shape* and *proportion* be arrested, and the transitional form unchanged. In a specimen given by Dr. Murphy, of a female adult pelvis, the diameters were *above* the standard size, but the antero-posterior diameter was 5½ inches, and longer than the transverse; the transverse of the outlet proportionately diminished; the cavity shallow; and the general form of the pelvis infantile; but the bones perfectly ossified. The pelvis has the shape and proportions of that of a child, and the size of an adult female (*see fig.* 113.). To judge from the appearance of this specimen, as seen in the drawing given by Dr. Murphy, it seems to be a pelvis in which the transverse processes of the last lumbar vertebra are enlarged, ankylosed to the sacrum, and articulated with the ilia, giving the appearance of five sacral holes instead of four. This would account for the increased antero-posterior diameter, and apparent elevation of the sacrum. Cases of this kind are more especially described in the latter part of this article.

Dr. Knox has observed that the male pelvis also sometimes permanently retains the infantile form, to which it is normally more approximated than the female. In one of this kind in his possession, the greatest transverse diameter was nearest the sacrum, and only ⅘ths of an inch larger than the conjugate.

Fig. 113.



Adult pelvis of infantile form. (*After Murphy.*)

Masculine pelvis.—In females of a robust frame and powerful development of muscle, and accustomed to hard masculine labour, the pelvis often presents the character of the male in many important respects. The transverse measurement of the brim is proportionately smaller, the antero-posterior diameter being often increased, and the shape of the brim is thus rendered more oblong; the sacrum is narrower, the pubic symphysis longer, and the cavity deeper, and rendered *funnel-shaped* and less roomy, by the approximation of the ischial tuberosities; by which also the sub-pubic angle is diminished to 60° or 70°. The ischial spines are longer, stronger, and project more inwards; the ilia are less expanded, and the bones larger, more massy, and more marked than in the "*standard*" pelvis.

Dr. Knox is of opinion that in many instances the true pelvis may be of normal size, and yet the haunches be remarkably narrow, owing to a want of proportion of the true and false pelvis; so that while the walls of the latter are flat, upright, and approximated, the true pelvis is of proper dimensions. He adds, moreover, that the opposite dispropor-

* Op. cit.

† Dissertatio de Mutatione Figuræ Pelvis. Leyden, 793, p. 14.

tion sometimes is present, and may mislead the obstetrician by giving an apparent breadth of haunch, while the contraction of the true pelvis may be considerable. He considers it to result from the entirely different and independent development of the false and true pelvis.*

I have met with many specimens of the masculine form of pelvis in the dissecting-rooms, from among the laborious women of this metropolis. In Dr. Murphy's experience it is more common than had been hitherto supposed.

The obstruction in this form of pelvis is met with chiefly in the deep funnel-shaped cavity, at the projecting ischial spines, or at the inferior outlet, under the narrow arch, and between the tuberosities, and is rendered the more serious by the fœtal head in these cases being generally more ossified than usual. The great inward projection of the sciatic spines sometimes affords an obstacle to the passage of the head. The average normal distance between them will be found, on reference to the tables, to be 4 inches. During the turning of the head in the most frequent positions, the inter-temporal and inter-zygomatic diameters of the fœtal head, the former of which is placed by Dr. Murphy at 3 inches, and the latter at $3\frac{1}{2}$ to 4 inches, are placed obliquely between them. In one or two instances I have found the sciatic spines as near to each other as $3\frac{1}{4}$ inches, and in one it was not co-existent with any extraordinary massy or masculine proportions, but simply with small transverse diameters. In the fronto-cotyloid and fronto-pubic positions, or with a large fœtal head, the approximation of the sciatic spines becomes a serious impediment to labour. In this pelvis the sacro-coccygeal articulation is said by Dr. Murphy to be generally less moveable, and the sacro-iliac joints unyielding, and that a bony ridge is often found on the posterior surface of the narrow pubic symphysis.

The *cause* of this form of pelvis seems to be, an advanced condition of ossification in a pelvis which would otherwise have been "*infantile*," brought about by the development of unusual muscularity, corresponding to the laborious employment of the individual. This action of the pelvic muscles will have also the effect of impressing irregularities upon the bones into which they are implanted, or over which they act. The tension of the posterior spinal and abdominal muscles against those of the leg would tend to elongate the pelvis, while the powerful great glutei, much used in supporting or raising heavy weights, will press inwards the ischial tuberosities, and narrow the sub-pubic arch.

Irregularities of the pelvi-vertebral angle.— Too great obliquity of the pelvis has been said to cause "*ante-version*," by throwing the weight of the uterus on the anterior abdominal walls; and too little obliquity to have a tendency to produce prolapsus uteri. Naegele (*Das weibliche Becken*), however, considers many of these supposed consequences are theoretical only; but he observed, both in first, and after many labours, that an approximation of the pelvic plane to the perpendicular caused the fœtal head to be placed so much forward, and the os uteri so high, as to be felt with difficulty; and, on the other hand, in very considerable inclination to the horizon the fœtal head was deep, and not easy to be felt through the uterine neck. In neither condition was there any important deviation from the mechanism of natural parturition.

The alteration of the planes of the pelvic outlets becomes, however, a valuable means of indication of the more important class of pelvic distortions, in which such an alteration is generally effected. In particular, when the tip of the coccyx and pubic symphysis are unusually placed, especial attention to the form and measurements of the pelvis is called for; though, as before seen, an alteration of the pelvic planes alone does not necessarily imply a distorted pelvis.

Dr. Rigby mentions, that the pelvic inclination is generally less in a tall slender person than in a short thick-set woman; and that, in the former case, the hollow of the sacrum is generally small, and in the latter deep.

2. *Distortions* of the pelvis are best arranged into the following practical divisions, according as they affect the *brim*;—the *cavity*;—or the *outlet* only or principally;—or the *whole structure* of the pelvis at the same time.*

Distortions affecting the brim only or principally.— By far the greater majority of these cases consist in an unusually *forward projection* of the *sacral promontory*. This causes the opening to assume a *heart-shape*, diminishes the conjugate diameter, sometimes contracting also the oblique, and increasing the transverse in some degree. At the same time, the promontory of the sacrum is sunk down below its normal altitude, lessening the angle of the superior plane, and making its axis assume a more vertical direction. Most generally the sacral projection deviates from the medium line, and forms the lower extremity of an abnormal curve in the lumbar vertebra, rendering the brim of the pelvis generally unsymmetrical in shape.

This deviation takes place most frequently, according to my own observation, to the *left* side, and appears to be an exaggeration of a very common tendency (which, being seen in the most robust subjects, can scarcely be called abnormal) of the natural curve of the lumbar vertebra towards the left side. This lateral curve is evidently a compensatory one to the very usual and well-known deviation of the

* Med. Gazette, vol. xxxii. pp. 555. and 589.

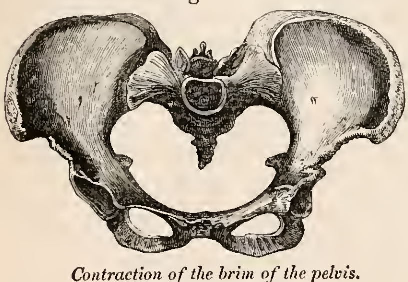
* Osiander enumerates six forms of pelvic deformity, classified without regard to their origin or bearing upon parturition; viz. 1. The *elliptical*, with diminished antero-posterior diameters, and without projection of the sacral promontory; 2. The *reniform*, with a sacral projection; 3. The *hourglass* or 8 *shaped*, from a curve backward at the symphysis pubis; 4. The *oblong*; 5. The *oblique*; and 6. the *angular* or *triangular* form. The method of arrangement I have adopted in the text, seems, however, the best adapted for useful applications.

line of thoracic vertebra to the *right* side, and is calculated to keep the line of the whole spinal column in equivalent relation to the direct and perpendicular line of gravity. It is an interesting question, how far this common tendency of the lumbar curve influences the position of the fœtal head, by affording more room for the sinciput at the right sacro-iliac joint, and determining its long axis in the left oblique diameter, which is generally allowed to be the most frequent presentation. In by far the greater number of all kinds of pelvic deformity that have come under my own observation, the projection of the sacral promontory, when present, has been towards the left side, showing the effect of a natural and previously existing tendency when the supporting structures have been softened by disease. To this subject I shall presently have occasion again to advert.

In these cases of partial distortion of the pelvic brim, the cavity and inferior outlet are generally roomy, shallow, and open. Often the transverse or antero-posterior diameter of the inferior outlet is larger than natural, and the pelvis then approaches the condition of the complete *ovate* deformity. An important practical result of this fact is, that in these deformities of the brim all operations for extraction of the fœtus "*per vias naturales*" are facilitated and rendered more successful. The obstruction being simply and only at the brim, when that is overcome the rest is easy.

Two *examples* of deformity of the brim are recorded by Dr. Ramsbotham. One is preserved in the Museum of the London Hospital (*see fig.* 114.). The conjugate diameter of

Fig. 114.



Contraction of the brim of the pelvis.
(*After Ramsbotham.*)

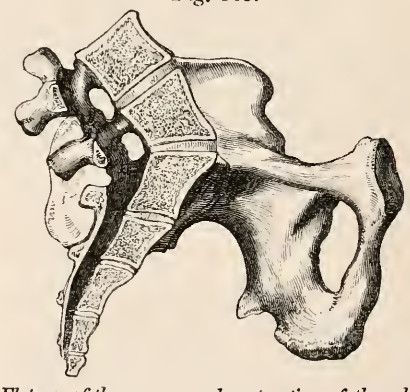
the brim measures $2\frac{3}{4}$ inches; the transverse 5 inches; and the distance from the side of the sacral promontory to the centre of the superior branch of the pubis on each side is equal, and measures also $2\frac{3}{4}$ inches. Dr. Ramsbotham considers this to be just below the smallest space through which the fœtal head could pass entire. The cavity, however, and the sacral curve, are well proportioned, and the distance between the sciatic tuberosities $4\frac{3}{8}$ inches, or a quarter of an inch more than in a healthy pelvis; so that the fœtal head would pass easily, having overcome the obstruction at the brim. The second is the pelvis of a woman who was delivered by craniotomy, which is considerably contracted in all its diameters, but more especially at the brim. The conjugate diameter is $2\frac{1}{4}$ inches only; the transverse $4\frac{3}{4}$ inches; and while the distance from the right side of the sacral promontory to the right pubic ramus is $2\frac{1}{2}$ inches, that on the left side is $2\frac{1}{4}$ inches only. The depth of the cavity posteriorly is only 4 inches; the spines of the ischia project considerably inwards, and the distance between the tuberosities measures only $3\frac{1}{4}$ inches.

This author considers that a proportionate increase in the transverse diameter does not fully compensate for a great contraction in the conjugate, in permitting the passage of the fœtal head. In cases in which the brim is oblong, and presents a preponderance of the antero-posterior diameter, as in the funnel-shaped and masculine pelves, the fœtal head necessarily presents its long antero-posterior diameter to that of the brim, and the case may be one of face presentation.

Distortions affecting the cavity only or principally, and causing obstruction there to the passage of the fœtal head.—These are occasionally seen without particular deformity at the brim or outlet.

Vertical flatness of the *sacrum*, or want of the proper vertical curvature, is occasionally met with, according to Dr. Churchill, after whom the annexed engraving of a specimen of this deformity is taken (*fig.* 115.). This is

Fig. 115.



Flatness of the sacrum, and contraction of the pelvic cavity. (*After Churchill.*)

sometimes accompanied by an increased sacro-vertebral angle. One or two instances I have met with, in which there was a tendency to this peculiarity. It is attended with diminution of the antero-posterior diameter of the cavity, and is most frequently met with in cases of general *ovate* deformity.

The opposition it would offer to the passage and circumvolution of the fœtal head is evident.

An *inward projection* of the *sciatic spines* is often seen in connection with contraction of the transverse diameter of the inferior outlet, without any inordinate massiveness or masculine form of the pelvis, as in the example before mentioned, and is, probably, sometimes dependent on the same cause—viz., the action of the great glutei muscles upon softened ischia. In some instances, however, this length and projection of the spines cannot be thus accounted for. Obstruction may occur before the head reaches the tuberosities in these cases. Their relative positions may be altered also by fracture.

Pelves in which the cavities are contracted at the lower part by *disease*, present the chief obstacles at the inferior outlet, and will be considered under that head.

A variety of the shape of the pelvic cavity is mentioned by Murphy, as forming a contrast to the funnel-shaped masculine pelvis. It is the funnel-shaped *reversed* by the gradual widening of the transverse diameters downward; but, being generally attended by some contraction at the brim, it belongs rather to the classes of deformities before described, and would seem to resemble the first case of Ramsbotham's there cited, and to be the beginning of a more complete ovate deformity, afterwards to be mentioned, as shown by the *widening* of the inferior opening.

Distortions affecting the outlet only or principally. — In these cases the greatest obstruction occurs at the inferior outlet, which, being comparatively independent of the brim and cavity, may be contracted without any important alteration in their shape or size.

Contraction of the *transverse* diameter is the most frequently seen. The ischial tuberosities are approximated, and the space of the sub-pubic arch lessened; and thus, indirectly, the antero-posterior diameter is rendered less effectual. Cases are frequently presented to the obstetrician, and many are on record, in which obstruction has occurred at the sciatic tuberosities, and the use of the forceps been rendered necessary. The normal distance between the centres of these processes is from 4 inches to 4½. In my measurements I have met with as small a distance as 3¾ inches in female pelves, in which the transverse diameters were generally rather small.

The bi-parietal diameter of the fœtal head is said to be 3½ inches, and is placed obliquely between these tuberosities, as the occiput emerges under the sub-pubic arch. The soft parts, besides, will occupy at least three-fourths of an inch. Thus with a large and well-ossified head and contracted intertuberal distance, the impediment is great. The diminished span of the sub-pubic arch, also, pushes back the head upon the coccyx, and renders a greater enlargement than usual of the antero-posterior diameter necessary; while at the same time the great sacro-sciatic ligaments are also approximated and rendered extremely tense, and thus the *oblique* diameter between them and the ischio-pubic rami is also considerably diminished.

The *special cause* of this deformity, when not dependent upon the infantile, masculine, or funnel-shaped pelvis before described, is to be attributed to the action of the great glutei muscles, in standing and walking, pressing upon the ischia partially softened by disease.

Contraction of the *antero-posterior* diameter. This results in most cases from *ankylosis* of the *sacro-coccygeal joint*. The coccyx is rendered immoveable and incapable of yielding to the head of the fœtus, so as to bring about the usual increase in the antero-posterior diameter. In addition, it is usually ankylosed in an almost *horizontal* direction, with its apex directed forwards and its surfaces upwards and downwards, a position which is brought about by the resiliency of the sacro-sciatic ligaments and ischio-coccygeus muscles, and by a continued sitting posture; — and thus the antero-posterior diameter is still more diminished.

The fœtal head is arrested by, and rests on, the coccyx, and the obstruction is only overcome by the giving way of the bone at or near the ankylosed part. The delivery generally requires instrumental aid.

Examples of this condition are numerous. In the practice of Dr. Michaelis of Kiel, a fracture of the parietal bone of the infant was occasioned by an immobility of the coccyx resulting from ankylosis.* Dr. Merriman, in a Letter to Dr. Lee, published in the Med. Gazette (1843, p. 224.), mentions a case in which the point of the coccyx snapped off in three successive labours, and he had observed one or two other cases in which this occurred, and no ill consequences followed. In one, the coccyx was turned upwards, and there was a considerable bulk of ankylosis, produced by a fall. Dr. F. Ramsbotham also mentions three instances in which fracture at or near an ankylosis of the coccyx took place. Dr. Lee relates also a case which occurred in the practice of a country surgeon, in which the lower end of the sacrum curved much forward and was ankylosed to the upper coccygeal bones, the last only being moveable.

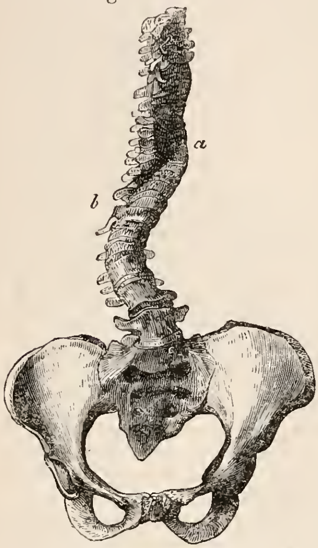
In certain cases the contraction of this diameter is brought about by the *tilting forward* of the lower end of the *sacrum*, with an almost horizontal direction of the lower part of the sacral curve. I have met with two or three pelves in which this condition is present, coexistent with, and evidently caused by, a curvature of the lower dorsal region of the spinal column *backwards*. By such a curvature, the line of gravity of the *trunk* is displaced backwards, passing through the sacrum considerably *behind* its base, and making traction upon it in that direction. The promontory of the sacrum is by this means dragged *backwards* and *upwards*, and the conjugate diameter of the brim increased, so as to be equal to, or greater than, the transverse. The shape of the brim is thus rendered *oblong* or oval in the opposite direction to, and contrasting with, the ovate deformity presently to be described. The axis of the superior plane is rendered more horizontal than normal, by the increase of the pelvi-vertebral angle, the cotylo-sacral arch more open in its curve, and the acetabula in some measure approximated. The cavity of the pelvis is narrowed antero-posteriorly by the gradual advance downwards of the posterior wall, and the vertical curvature

* Neue Zeitschrift für Geburtskunde, t. iv. 1836.

of the sacrum is more open than usual. Thus is constituted another variety of *funnel-shaped* pelvis, caused mainly by the gradually narrowing of *antero-posterior diameters*, instead of the lateral, as in the masculine pelvis before described.

In the King's College Museum are the pelvis and spine of a *female*, well exemplifying this deformity (see *fig*. 116.). The spine is affected by a rickety curve, the greatest extent of which is about the 6th, 7th and 8th dorsal

Fig. 116.



Oblong pelvic deformity. (*From a preparation in the Museum of King's College.*)

vertebræ (*a*), directed *backwards* to a great extent, and somewhat to the left side, with a compensatory curve to the right, at the junction of the lumbar with the dorsal vertebræ (*b*). The lower lumbar vertebræ and sacral promontory are twisted considerably towards the *left* side, and dragged backwards, the sacral promontory being also considerably raised upwards (*c*). The pelvis is of exceedingly large general capacity, and otherwise well formed, showing evidently, by the preponderance of the conjugate diameter and appearance of the sacrum, the effect of the deformed spine upon it. The conjugate diameter of the *brim* measures as much as 5 and a half inches; the transverse $5\frac{1}{8}$ inches. At the *outlet*, the distance between the tuberosities is only $3\frac{7}{8}$ inches, and the sub-pubic angle 75°; but, from an unfortunate deficiency of the lower end of the sacrum, the antero-posterior diameter cannot be measured.

In the same Museum there is a young *male* adult skeleton in which this form of pelvis is also well shown. It, also, is coexistent with, and dependant on, a backward curvature and shortening of the spine, and extensive ankylosis of the vertebræ in the dorsal and lumbar regions. The lumbar vertebræ are inclined much backward, so as to drag in the same direction upon the upper end of the sacrum; while the upper dorsal vertebræ incline forward, so as to bring the 1st dorsal over the centre of the pelvic circle. There is, in this case, no lateral deviation of the spinal column. The tibiæ and fibulæ have an inward curve, indicating the existence of a softened rickety state of the bones at an early period of life.

In the Hunterian collection of pathological specimens is a young adult pelvis, numbered 3420, presenting the same kind of deformity, accompanying the same kind of backward angular curvature and ankylosis of the bodies of the vertebræ at the same place — viz. the junction of the last dorsal and 1st lumbar. The 1st dorsal vertebra, in this skeleton, likewise occupies a position above the centre of the pelvic opening. The upper end of the sacrum is dragged backwards by the inclined lumbar vertebræ so as to increase the conjugate diameter of the brim to $4\frac{1}{2}$ inches. The lower end of the sacrum is tilted forward so as to bring the tip of the coccyx to within a short distance of the ischial spines. The cotylo-sacral arch is stretched out, and the transverse diameter of the brim reduced to 4 inches only. The acetabula are directed more downwards than usual, and the right iliac wing is pressed outwards by the 9th and 10th ribs, which rest on it, and the venter completely flattened out.

I find that Rokitansky has met with instances of this oblong deformity of the pelvis, coexisting with *backward angularity* of the spine.

In cases of backward angular curvature low down the spine, especially where there is no lateral deviation, there will be a tendency to production of this form of pelvis, especially if the bones be somewhat softened, as they usually are in these cases; and although such cases of pelvic distortion are, as far as I have seen, more common in the male, yet the same cause occasionally produces this effect upon the female pelvis, and may produce obstruction during parturition, not only by the contraction of the *antero-posterior diameter* at the *outlet*, but even at the *brim*, by the diminution of its *transverse diameter*.

An acute angle in the lower part of the *sacral curve* may also produce this contraction of the inferior pelvic outlet. When this exists singly, the elevation of the coccyx is more considerable than usual, and the axis of the inferior plane directed more backwards. This bending upwards of the apex of the sacrum is, however, most usually seen in connection with more general pelvic deformity, and is sometimes accompanied by ankylosis of the sacro-coccygeal joint.

In a case recorded by Mr. Bell, the antero-posterior diameter of the inferior outlet was contracted to half-an-inch only, and in one of Naegele's, it was even less than this, in both entirely precluding delivery. In so great a contraction, the sacral bend must have been unusually great, or the lower end of that bone tilted forward in the manner just described.

Distortions affecting the whole pelvis. — In these cases the pubic bones are always more or less extensively implicated in the distortion, and entering, as they do, into the formation of both brim, cavity, and outlet, all these parts of the pelvis are contracted or misproportioned. At the brim, however, the *obstruction* usually takes place, while the operations necessary to procure delivery through the natural passages are rendered more difficult by the distortion of the cavity and inferior opening.

General distortions of the pelvis are commonly divided into three kinds, named, from the shape of the brim, the *ovate* or *elliptical*,— the *cordiform* or *angular*,—and the *obliquely ovate.*

The ovate, elliptical, or reniform pelvis. — In this distortion the *sacrum* is placed almost horizontally, so that the sacral *promontory* projects forward to a great degree, generally at the same time deviating from the median line, and considerably sunk in a direction forwards and downwards, so that the lowest lumbar vertebra forms the most projecting point. The *lateral sacral curve* is diminished, flattened out, and often bent backwards on each side the promontory. The *vertical curvature* is generally diminished and flattened in some degree, and directed more downwards by the more horizontal position of the bone; but occasionally there is an acute bend forwards at the lower part. The *coccyx* is generally bent acutely forwards.

The *ilia* and *ischia* on each side are often removed to a greater lateral distance than normal. The *iliac wings* are flattened and directed more forward; and the *cotylo-sacral arch* is more sharply curved, and often shorter and thicker than normal. The *planes* of the *ischia* diverge instead of slightly converging downward; the *spines* and *tuberosities* being likewise divergent, and the latter directed more outwards and backwards. The *superior rami* of the *pubes* are generally flattened out, having little anterior projection; while the *inferior rami* are widely divergent, affording a wider and shallower expansion of the *sub-pubic arch.* In some cases, however, the sub-pubic arch is little altered.

In some instances the *symphysis* of the *pubis* presents the appearance of being indented or pushed backwards, giving an outline to the brim of an *hour-glass* shape.

The *diameter* principally diminished is the *conjugate* of the *brim,* and often one or other of the *oblique* diameters. In one variety the *transverse* diameter of the brim is also contracted. The transverse diameter is, however, sometimes undiminished, or even increased. The *transverse* diameter of the *inferior outlet* is generally most considerably increased; but the *antero-posterior* diameter is most usually contracted by the bend in the sacrum. In many instances, however, it is considerably enlarged. The *depth* of the true pelvis is generally diminished, and its capacity lessened.

The *sacro-vertebral angle* is generally much diminished, from the backward horizontal direction of the upper end of the sacrum.

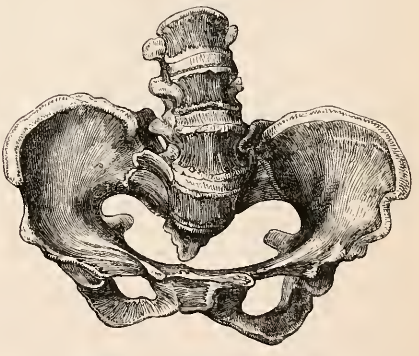
The *inclination* of the *superior plane* is sometimes increased so much as to be vertical; the *axis* of the brim being generally directed more forward than in the "*standard*," and that of the *inferior outlet* more backward. Sometimes, however, they are very little altered.

The *structure* of the bones is light, slender, and fragile, indicating the origin of the distortion in rickety softening.

Examples of this kind of pelvis are numerous. One of the most well-known is that of Elizabeth Sherwood, who was delivered by Dr. Osborne by means of the crochet. The measurements of this pelvis are given as follows:—From the most prominent point of the lumbar vertebra to the upper border of the pubic symphysis, $1\frac{1}{8}$ inch. From the same point on the left side to the left pectineal eminence, $1\frac{6}{8}$ inches. The same measurement on the right side, $1\frac{7}{8}$ inches. From the sacral promontory to the pubic symphysis, $1\frac{1}{4}$ inch. Transverse diameter of *brim*, 5 inches. Left oblique ditto, $4\frac{1}{4}$ inches. Right oblique, $4\frac{1}{2}$ inches. Antero-posterior of *cavity*, $2\frac{1}{4}$ inches. Transverse ditto, 5 inches. Antero-posterior of *outlet*, $2\frac{7}{8}$ inches. Transverse, $4\frac{1}{2}$ inches. Sub-pubic angle, 100°.

The measurements of a very extreme case of this kind of distortion are recorded by Dr. Ramsbotham (see *fig.* 117.) as follows: —

Fig. 117.



Ovate pelvis. (*After Ramsbotham.*)

Conjugate or sacro-pubic diameter of *brim*, $\frac{3}{4}$ of an inch only. From right side of sacral promontory to right pubis, $1\frac{1}{4}$ inch. The same measurement on the left side, $1\frac{5}{8}$ inch. Antero-posterior diameter of *outlet*, 2 inches. Transverse diameter, $4\frac{1}{8}$ inches. The shape of the brim in this pelvis is hour-glass, the pubic symphysis being pushed back. Such a pelvis, in the opinion of the above-named writer, would necessitate the abdominal section.

In a less extreme case, given by the same writer, the sacral promontory and lumbar curve bend much more considerably towards the *left* side. At the *brim*, the conjugate diameter is $1\frac{1}{2}$ inch; the right sacro-pubic, 2 inches; the left, $\frac{3}{4}$ of an inch only. The transverse diameter, measured in the lateral curve of the brim, $6\frac{1}{4}$ inches. At the *inferior outlet*, the antero-posterior, $4\frac{1}{2}$ inches; the transverse, $5\frac{1}{4}$. In the figure of this pelvis given by the author, the long axis of the sacrum is represented as placed obliquely across the median line, its apex inclining to the right side; while the tuberosity of the right ischium is widely divergent, principally causing the increase of the transverse diameter of the outlet. The left ischial tuberosity and acetabulum are brought more under the line of gravity. The left superior pubic ramus is thus pushed nearer to the promontory than the right, causing a slight twist in the pubic symphysis. In this pelvis the author considers that delivery might be effected "per vias naturales," by craniotomy.

In one of Dr. Hull's cases, that of Ann Lee, affected with this deformity, the conjugate diameter was reduced to $1\frac{5}{8}$ inch, and the sacro-cotyloid on each side equal, and measuring $1\frac{9}{16}$ inch. The transverse diameter, in its widest part, amounted to $4\frac{1}{4}$ inches only. There was little flattening of the pubes, the contraction being produced chiefly by the projection of the sacrum, the chief bend being near the sacro-iliac joints. The distance between the antero-superior iliac spines was only $8\frac{1}{2}$ inches, but the dimensions of the cavity and inferior outlet were not materially diminished.

In Mr. Thomson's case of Cæsarian section, the pelvis was affected with this deformity. The normal lumbar curvature was so much increased, together with the pelvic inclination, that the sacrum was placed quite horizontal, and the superior plane directly *vertical*, and its axis consequently parallel with the horizon; but with little or no lateral deviation of the sacral promontory. The legs were crooked, and the acetabula faced directly forwards. The conjugate diameter of the brim was diminished to $\frac{7}{8}$ of an inch; the transverse was about 5 inches, and the intersciatic apparently about $4\frac{1}{2}$.*

Dr. Robert Lee gives the dimensions of a case of ovate deformity in which the patient, after being delivered by craniotomy at an early period of pregnancy in the first labour, died in the second from rupture of the uterus. The conjugate diameter of the *brim* was 2 inches 1 line; the transverse, $5\frac{3}{4}$ inches. At the *outlet* the distance between the sciatic tuberosities was $4\frac{1}{2}$ inches; between the tip of the coccyx and lower border of the pubic symphysis, $3\frac{1}{2}$ inches. This obstetrician considers that if, in this case, premature labour had been induced at or before the fifth, instead of the seventh month, the patient might have been saved.†

It has been said that in pelves presenting the ovate deformity from rickets, the contractions of the diameters of the *brim* are generally accompanied by the *enlargement* of those of the *outlet*, and the numerous examples of enlarged transverse diameters of the outlet, in particular, are adduced.

In an ovately deformed pelvis in the Museum of King's College, however, in which the conjugate diameter of the *brim* is 2 inches, and the transverse also contracted to $4\frac{3}{4}$ inches; at the *outlet* the inter-sciatic diameter is *contracted* to as little as $3\frac{7}{8}$ inches, and with it the subpubic angle is diminished also, while the antero-posterior is *increased* to $4\frac{1}{4}$ inches. This pelvis is remarkable for the great flattening of the sacrum, the anterior surface of which lies almost in a straight line, in which direction the coccyx also is nearly placed. The antero-posterior diameter of the *cavity* is thus reduced to $3\frac{1}{4}$ inches. The distance between the ischial spines is, however, 4 inches. The sacral promontory projects more *forwards* than downwards, and the lumbar curve is inclined to the left side. In this pelvis the brim is contracted considerably in all its diameters, and this contraction is evidently produced by the crushing downwards of the sides of the cotylo-sacral arch. The length of the cotylo-sacral rib on the right side, taken from opposite the ilio-pectineal eminence to the sacro-iliac angle *along the curve*, amounts to only $1\frac{1}{2}$ inch, while the *direct* measurement is reduced to $1\frac{1}{8}$ inch. The rib of bone is at the same time much increased in thickness, presenting an almost cubical mass between the cotyloid and sacro-iliac articulations. On the left side, the *direct* measurement is a little more.

In the table of measurements of diseased pelves given by Dr. Murphy, the transverse diameter of the brim in the five ovate pelves amounts to 5 inches only in two cases, and in a third, it is diminished to $4\frac{5}{8}$ inches. In many of these cases we may conclude that the cotylo-sacral rib was shortened as well as bent backward. The transverse diameter of the inferior opening is not enlarged in all the above-mentioned cases. In one it amounted only to $3\frac{5}{8}$, and the sub-pubic angle (mainly depending on this diameter) is only 70°. The antero-posterior diameter is, in three cases, *increased* to from 4 to $4\frac{5}{8}$ inches, while in the remaining two cases it is diminished to $2\frac{1}{4}$ and $2\frac{7}{8}$. These latter measurements, doubtless, depend in great measure upon the position of the coccyx, or, as in the case above given from the Museum of King's College, upon the flatness of the sacrum, or in its bend. They show, however, that the enlargement of the inferior diameters in not universally characteristic of the general ovate deformity. We may also conclude that the general contraction of the diameters of the brim, which is often found in these pelves, is produced mainly by the *shortening* of the *cotylo-sacral rib* of the ilium in the line of pressure, without any *eversion* of the lower part of the innominate bones.

A singular pelvic deformity, related in some degree to this class, is represented in Moreau's plates, in which, by an anterior

* Med. Observations and Inquiry, vol. iv., with plates.

† Lectures in Med. Gazette, 1843, p. 181.

bend at the lower lumbar vertebræ, the sacrum is placed horizontally backward, and the sacro-vertebral angle diminished to rather less than a right angle. The effect of this is to increase the obliquity of the innominate bones, and the distance from the sacrum to the pubis, to approximate the pubis and coccyx, and to *widen* the transverse diameters. With the exception of the last-named peculiarities, this pelvis presents the condition and appearance of that of a quadruped, in being placed horizontally; the trunk, however, being kept in the vertical position by the remarkable sacro-vertebral bend.

The cordiform or angular pelvis. — This distortion presents wide differences to the kind just described.

The *sacral promontory*, though in some measure projecting forwards, yet is more decidedly sunk down below its proper level into the cavity of the pelvis, with an inclination to one side of the median line, in most cases to the left. The *lateral masses* of the *sacrum* are likewise bent back, altering the outline of the lateral sacral curvature. The *vertical curvature* of the sacrum is also increased to a great degree ; the *hollow* of the sacrum, in many cases, being almost bent double. The *coccyx* is generally placed horizontally.

The *ilia* and *ischia* on each side are pushed together upwards and towards the sacrum, so that the *acetabula* are thereby approximated and placed nearer to the sacral promontory. The *cotylo-sacral arch* presents, in most instances, a very sharp curve near the sacro-iliac joint, and is often bent double, so as to offer a mere chink between the sacral and iliac portions. The *iliac wings* are generally approximated, the *venter* being sometimes doubled into a mere fissure, and the *crest* being curved inwards more than normal, so as to bring the anterior superior iliac spines nearer together ; while the posterior extremity of the crest, or *iliac tuberosity*, is bent inwards and forwards over the sacrum, by the weight of the body, acting through the sacro-iliac ligaments. The *planes*, *spines*, and *tuberosities* of the *ischia* are pushed inwards towards each other, and sometimes turned more upwards, so as to cause a chink or acute bend in the ischial plane, passing downwards and forwards, and which has been compared by Naegele to the fold made by bending pasteboard. The *superior rami* of the *pubes* are directed horizontally forwards, being almost, and, in extreme cases, quite parallel to each other anteriorly.

This alteration in the direction of the pubic bones takes place, in many cases, by an inward curve in the acetabula at the point of junction of the three pieces of the innominate bone, as indicated by the ilio-pectineal eminence, and the form of the brim will then assume the shape of the letter Y when the deformity is great. In many instances, however, the superior pubic rami are bent inwards at an obtuse angle, in the *centre*, just above the obturator foramina, the bones of the opposite sides almost or entirely meeting at the angle, and continuing parallel with each other to their articulation. The form of pelvis resulting from this bend in the superior pubic ramus has received more particularly the name of the *cocked hat* or *rostrated* pelvis; the latter name being applied from the beak-like projection of the pubis at the symphysis. It is markedly distinguished from those angular deformities in which the inward bend of the innominate bones takes place at the acetabular junction of their three component pieces, and is found exemplified in most of the specimens exhibiting the greatest contraction of the diameters.

The *pubic symphysis* is, in every case, more or less folded back, straining upon the anterior ligaments. The bending, however, is seen to occur in the osseous portions of the articulation forming the pubic angles, generally about the position of the pubic spine, and it is much more considerable in the cases where the anterior portions of the pubes are parallel to each other. The *sub-pubic arch* is, in all cases, very considerably narrowed by the parallel position of the superior pubic rami and the approximation of the ischial tuberosities. In many instances, the latter appear to be pushed forwards and upwards, so that the contraction of the sub-pubic arch is greatest at the ischial rami, just above the tuberosities, above which point the sides of the arch bulge outwards. In the *rostrated* pelvis, it is often completely obliterated or transformed into a mere chink. The *acetabula* are elevated and turned more forwards than normal, and in many examples of rostrated pelvis are directed almost quite anteriorly.

The *angles* of both the *superior* and *inferior pelvic planes* with the vertebral column are lessened. In a case given by Naegele, the superior plane was at right angles to the spine. The *axis* of the *brim* is thus rendered more vertical, and that of the *outlet* more forward, than in the standard pelvis. The superior plane is often bent into two by the elevation of the acetabula, but, in some instances, the pubic symphysis is pushed upwards above the acetabula.

The *diameters* are all contracted in a greater or less degree, those of the brim most extensively. In this kind of pelvis occurs the greatest diminution of diameters of all the recorded examples. The diminution, however, is such, that if the irregular form were reshaped, the diameters would be replaced, *i. e.* there is no absolute shortening of the bones, or not so much as in the rickety pelves.

Examples.—The pelvis of Isabel Redman (*fig.* 118.), upon whom hysterotomy was performed by Dr. Hull in 1794, and which is said to present at the brim the most contracted diameters on record, is affected by this deformity in its rostrated form to such an extent, that a ball $1\frac{3}{8}$ inch in diameter would not pass through it at any part.

At the *brim*, the 4th lumbar vertebra was completely sunk into the pelvis, and inclined to the *left* side, and its distance from the pubic symphysis was $2\frac{3}{10}$ inches. The distance between the superior pubic rami at

Fig. 118.

Pelvis o Isabel Redman.

the point of angular bend, was $\frac{7}{8}$ of an inch. From the 4th lumbar vertebra at its upper anterior border, to the left acetabulum, was only $\frac{5}{8}$ of an inch; on the right side $\frac{7}{8}$. The greatest transverse diameter was $5\frac{2}{8}$ inches. At the *outlet*, the distance between the sciatic tuberosities was $3\frac{3}{4}$ inches; between the spines $2\frac{6}{8}$. The greatest contraction of sub-pubic arch was at the sciatic rami, which were only $\frac{7}{10}$ of an inch distant from each other; above this, the arch bellied out. The sacrum was bent double, so that the tip of the coccyx was only $1\frac{1}{10}$ inch from the sacral base. The pelvic bones were quite soft, and lighter than natural.

The measurements of the pelvis of Jane Foster, who was saved by the Cæsarian section by Mr. Barlow, are given as follows:—From the fibrocartilage between the 4th and 5th lumbar vertebræ (which is sunk down so as to occupy the normal position of the sacral promontory), to the outside of the projecting pubic symphysis, is 3 inches. From the same point, to the centre of the superior ramus of right pubes, $\frac{7}{8}$ of an inch, of clear available space. The same measurement on the left side, $1\frac{3}{8}$ inch. From the same point, to the right acetabulum $\frac{3}{4}$ of an inch; to the left acetabulum $1\frac{1}{4}$ inch. The greatest available space is, from the left side of the sacral promontory to the left ilium, and amounts to $1\frac{1}{2}$ inch. The greatest lateral space, following the curve, is $5\frac{3}{8}$ inches. At the *outlet*, the distance between the sciatic tuberosities is $1\frac{1}{2}$ inch. The coccyx and lower part of the sacrum are bent upwards, so as to bring the tip of the coccyx to within $1\frac{1}{2}$ inch of the sacral promontory, and to $2\frac{1}{2}$ inches from the point of contact of the ascending ischial rami, which are so close as to obliterate entirely the sub-pubic arch.

The dimensions of the *rostrated* pelvis of Elizabeth Thomson, who underwent the Cæsarian section at the hands of Mr. Wood of Manchester, and died in consequence, are given by Dr. Murphy, as follows:—From the most projecting point of the sacral promontory to the pubic symphysis, 2 inches. From the same point to the left pectineal eminence, $\frac{5}{8}$ of an inch; to the right pectineal eminence, $\frac{5}{8}$ of an inch. The transverse diameter of the brim, $2\frac{1}{2}$ inches; both the oblique, $3\frac{1}{4}$ inches. *Cavity:*—antero-posterior diameter, $3\frac{1}{8}$ inches; transverse diameter, $2\frac{3}{4}$ inches. *Outlet:*—antero-posterior diameter, $3\frac{1}{2}$ inches; transverse diameter, $2\frac{6}{8}$ inches. The sub-pubic arch measured 10° only.

In a specimen of rostrated pelvis given by Dr. Ramsbotham, the antero-posterior diameter of the *brim* is diminished by the projection of the sacral promontory, and the bend in the pubis, to $1\frac{5}{8}$ inch. The same measurement on the left side of the promontory, $2\frac{3}{8}$ inches; on the right side, $2\frac{1}{2}$ inches. The longest transverse diameter is $4\frac{1}{2}$ inches. At the *outlet*, the nearest points of the ischial tuberosities are as close as $1\frac{3}{4}$ inch; but from the tip of the coccyx to the lower border of the pubic symphysis measures $4\frac{1}{2}$ inches. In the opinion of this author, a fœtus might be extracted from this pelvis by craniotomy.

In Dr. Cooper's case of Cæsarian section, the pelvis was affected with the angular deformity to the extent of reducing the conjugate diameter of the *brim* to $1\frac{1}{4}$ inch.; and the transverse diameter of the *outlet* to $\frac{1}{2}$ an inch only.*

In Dr. Kellie's unsuccessful case of Cæsarian operation, the pelvis was of the *rostrated* kind; the superior pubic rami being as if fractured in the centre, and held only by ligament. The lumbar curve was to the right side, and the 4th vertebra was sunk below the plane of the pelvic brim. The right lumbo-cotyloid diameter was only $\frac{8}{10}$ of an inch; the left, $1\frac{2}{10}$. Between the lumbar vertebra, and the bend of the pubic rami, was only $\frac{8}{10}$ of an inch. At the *outlet*, the intersciatic distance was only $2\frac{7}{10}$; antero-posterior, $3\frac{4}{10}$ inches. The sacrum was doubled, so that the tip of the coccyx was but 1 inch from the sacral base. The pelvic bones were soft; but the joints and cartilages healthy. In this case, the patient was only twenty-seven years old, and had borne four children: the last, three years before her death.

In Dr. Radford's two unsuccessful cases of hysterotomy, the deformities were both from malacosteon, and the form *rostrated*. In one, the circle of space at the brim was only about $\frac{3}{4}$ of an inch in diameter; the opening Y-shaped. The distance between the sciatic tuberosities was $1\frac{1}{2}$ inch, and the sub-pubic arch reduced to a small slit. The subject had previously undergone nine natural deliveries, and one by craniotomy. In the other case, the conjugate diameter was reduced to $\frac{3}{4}$ of an inch; and the superior rami were also bent so as to be parallel anteriorly. The patient had borne seven children with great ease previously; the last case four years before the operation.†

Dr. Hamilton's case was also *rostrated*, the

* Med. Observ. and Inq. vol. v. p. 218.
† Edinburgh Med. and Surg. Journal, vol. lv.

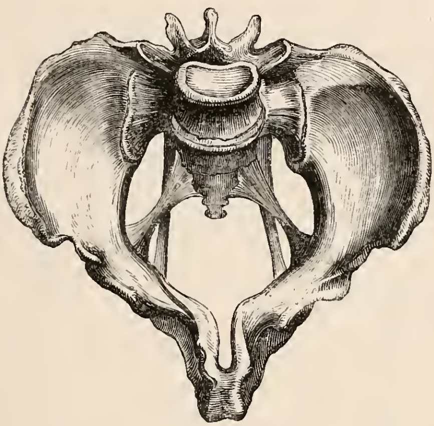
pubic rami being approximated at the angular bend to $\frac{5}{8}$ of an inch.

In a case which was operated on by Dr. Hæbeke, and described in *L'Experience* (No. 140.), the inferior pelvic outlet was nearly closed up entirely, the ischial tuberosities being approximated to within two lines only, and the coccyx and pubes admitting only one finger between them.*

In Mr. Kinder Wood's case, the deformity was *rostrated*, the most available space at the *brim* being a circle of 1 inch diameter to the left of the projecting promontory. The antero-posterior diameter was $1\frac{1}{2}$ inch, but less than $\frac{3}{8}$ of an inch when the soft parts were attached.†

A somewhat remarkable variety of the *rostrated* pelvis is figured by Dr. Churchill (*fig.* 119.). In this pelvis the *superior pubic ramus*

Fig. 119.



Oblong rostrated pelvis. (*After Churchill.*)

is bent at its centre, so as to be nearly approximated to the opposite pubis at that point, and the *symphysis* projects in a rostrum. The upper part of the *sacrum* and the *promontory* is, however, thrown back, the *cotylo-sacral arch* spread out, the *antero-posterior* diameter increased, and the *transverse* lessened, somewhat in the same manner, and, doubtless, by the same mechanical conditions, modified only by the yielding of the pubis, as in the *oblong* pelvis before described. The *acetabula* in this pelvis are directed principally forwards and outwards.

Causes of the foregoing pelvic distortions.—The principal causes of the preceding partial and complete distortions of the pelvis, are two diseases affecting the osseous system; viz. "*rickets*"—and "*mollities ossium*" *or* "*malacosteon*."

Rickets is a very common disease of early life, which is said to be more apt to occur in scrofulous children about the period of dentition, but which may occur even after puberty, according to some authors. It is characterised by a simple deficiency of the earthy matter of the bones—chiefly of phosphate and carbonate of lime; while the animal constituents, although softened, and rendered less elastic, retain nearly their normal composition. The bones thus rendered pliable, which lie in the lines of weight, pressure, or muscular action, yield slowly and give way to the operating forces, bending in such a manner as the resultant direction of pressure and muscular traction, &c., permits them.

We must refer the reader to the Article on the Pathology of Bone (vol. i. p. 440.) for a more detailed account of this disease.

In Rokitansky's Pathological Anatomy, the bones in *Rhachitismus infantalis* are described to present two separate pathological conditions. In one, the bones are very vascular, soft, fragile, and swollen, with enlarged medullary cavities, and the areolar spaces filled with, and often distended by, a pale, reddish jelly, which pressing upon the areolar partitions, produces their absorption, and thus the enlargement of the cavities by coalescence. This jelly is also sometimes found effused under the periosteum. In the second variety, the bone is more or less reduced to its cartilaginous elements, the corpuscles (*lacunæ*) empty, the rays obliterated, and the lamellar structure wanting, or fallen asunder, with corpuscles interposed between the layers. On the last condition the softening of the bones depends. The periosteum is more vascular than normal, tumid, and more closely adherent, so as to tear off with it a portion of the softened adjacent bone. It is said to differ from malacosteon in not being a painful disease, and in being capable of cure, with a subsidence of the swelling and reabsorption of the effused substance. In high degrees of the disease, however, atrophy and fragility remain permanently. The osseous structures affected by rickets are lighter, less marked, thinner, and more porous than normal, or than those affected by mollities ossium, according to Naegele;—appearing as if they had been steeped in weak acid.

The analysis of a rickety humerus and scapula, is given by Rokitansky as follows:

Phosphate of lime and magnesia -	15·60
Carbonate of lime - -	2·66
Soluble salts - - -	0·62
Total of inorganic matter -	18·88
Cartilage, vessels and fat -	81·12
	100·00

In the humerus, also, was found 10·54 per cent. of fat. Specific gravity of the bone, 0·612.

Davy found in 100 parts from the tibia of a rickety child, 74 parts animal and 26 earthy; and Bostock, in a vertebra affected with the same disease, 79·75 animal, and 20·25 earthy, in 100 parts.

When this is contrasted with the norma proportions of the osseous constituents in the child, as given by Schreger—viz. 47·20 parts animal, and 48·48 earthy (or about one half

* Lancet, 1840.

† Med. Chir. Trans. vol. vii. p. 264.

of the weight of the bone) in 100 parts—the great diminution of the earthy matter will be evident.

In *rickets* the bones of the lower extremities first exhibit deformity, which appears chiefly as an aggravation of the natural curves under pressure, and as a yielding in the direction of the lines of muscular motion. The femurs, for instance, are bent, in most cases, with the convexity forwards and a little outwards; the tibiæ and fibulæ generally with the convexity forwards and inwards, so that the knees are bent inwards and the feet thrown outwards and backwards (see *fig.* 122. B and E.) The bones of the pelvis and spine become affected, and those of the upper extremities, ribs, and head afterwards follow.

The spinal column may be extensively deformed, especially at its upper part, without any deformity whatever of the pelvis. An example of this is to be found in the Museum of King's College, and many in the Hunterian Museum. Many others are also recorded. In most of these cases, however, the special curvature results from caries of the vertebræ, or lateral curvature.

Meckel remarks, that spinal curves resulting from general disease of the bones, such as rickets, are usually accompanied by pelvic deformity. The lumbar portion of the spine is curved forwards and sideways, the thoracic portion backwards; and sometimes, the bodies of the vertebræ become affected with caries, and produce angular curvature and ankylosis. The sacrum at the same time sinks under the weight of the spine, and the pelvis becomes impressed, generally, with the complete *ovate distortion*, or one of the partial deformities of brim, cavity, or outlet, which are its commencements. In a good many cases, however, as we shall presently see, the rickety pelvis assumes the *angular* form of distortion; and, in some, the *oblong* form previously described. It is, however, universally shallow, contracted, and of small capacity. The iliac wings are thin, and present a greater central area of translucency than usual; while the columnar masses of bone are shorter, lighter, and less dense, but often present, as we have seen in the *ovate* pelvis with universally diminished diameters, a *thickening* of their bulk, corresponding to the shortening they have experienced by pressure.

Rokitansky mentions that this thickening takes place in common with all the osseous structures abounding in diploetic tissue. In many instances, it evidently depends upon the excess of reparative osseous deposit, described by Stanley as taking place in the lines of the greatest pressure. In all the specimens I have examined, it takes place by far the most considerably in the cotylo-sacral rib, through which the greatest amount of pelvic pressure passes. Shaw pointed out that in most rickety deformed pelves, the contraction of the diameter at the brim is universal as well as disproportionate, from the absolute shortening and *atrophy* of the bones. In fourteen rickety femal adult pelves, he found a general deficiency, in the measurements of the bones, of one quarter of the whole normal size. He also found that the bones of the lower extremity generally are atrophied in this disease more than those of the upper.* Rokitansky also considers rickets to interfere with the general development of the bone.

Mollities ossium or *Malacosteon adultorum* is a disease, not very frequent, affecting the full-grown adult skeleton. It most commonly affects the female sex about the middle period of life, but seldom, according to Rigby, attacks women who have had no children. Three instances in which this disease occurred in the male subject are, however, given by Mr. Curling in the Med. Chir. Trans. (vol. xx. p. 360.). Nor does it seem to be confined to middle age—in Kellies' case, the woman was aged only twenty-seven years—nor to parturient women, as will be seen in Mr. Solly's case.

In many cases, it is said to depend upon the cancerous diathesis, and to result from the dissemination of cancerous matter throughout the system, infecting the nutrition of the animal matter of the bones, and replacing the earthy constituents; thus causing the osseous structures to lose their cohesive power. By far the greater proportion of the complete cases of pelvic deformity, as well as the most extreme and universal contraction of diameters, have resulted from this disease.

For the particular pathological instances of this remarkable disease the reader is referred again to the article on the Pathology of Bone (p. 442. vol. i.) In addition to the cases there described, may be mentioned one which was brought before the Med. Chirurgical Society by Mr. Solly, and published in vol. xxiii. of the Transactions (p. 437.). The subject was a female who had never borne children, and the fragility of the bones appeared at as early an age as twenty-two. She had violent pains in the back, and a white sediment in the urine. At the age of twenty-four, the spine began to yield, and she had rheumatic pains in the head. At thirty-six years, the catamenia ceased, and the patient began to be unable to walk or stand, and had great pain; the greatest deformity being then apparent about the hips and shoulders. The bones of the head then became thickened, and those of the lower extremities more curved, and fractured by the slightest force; but the urine at this time was clear and natural. The patient died, worn out by the disease; and post-mortem examination showed the long bones to be reduced to mere outer shells, which could easily be cracked by pressure with the finger and thumb. The interior was filled with grumous matter, of hues varying from dark blood to light liver-colour. Both the femurs were broken, the tibiæ and fibulæ bent, the spine much curved, and the pelvis extremely reduced in its diameters; but the joints and cartilages were all healthy. The cranial bones were much thickened, and so soft as to be easily cut with a knife. The

* Med. Chir. Trans. vol. xvii. p. 434.

diploe was obliterated, the Haversian canals enormously enlarged, and the osseous corpuscles (*lacunæ*) diminished in quantity. From an analysis made by Dr. Leeson, the fresh bone contained,—in 100 parts; animal matter, 18·75; water, 52·08; phosphate and carbonate of lime, 29·17 parts. The grumous medullary matter contained,—in 100 parts; animal matter, 24·78; water, 73·39; and phosphate and carbonate of lime, 1·83 parts. Under the microscope, Rainey found many granular, roundish bodies, about the size of blood corpuscles, and some fat globules;—Simon, in a different part, could find no new or mature cell formations, but plenty of cytoblasts, and a few young fat cells.

Mr. Curling considers the softening of mollities ossium to be *eccentric; i. e.*, to commence in the centre of the bone, and pass outwards, affecting first the denser parts, and then the areolar extremities of the bone. He looks upon it as the result of defective nutrition, and that both the constituents waste in nearly equal ratio throughout. This author remarks that the pains always *precede* fracture or distortion, and are not the *result* of these conditions. In one case, he observed copious sweats and salivation; in another, a fœtid unctuous exudation from the hands and feet; in a third, fœtid perspiration; in a fourth case, that of an old woman of seventy, who had been bedridden for four years from paraplegin, there were no deposits in the urine. The pelvic bones might be cut with a knife, but the ribs and vertebræ were less affected. The enlarged cavities and areolæ were filled with red patches, resulting from injected vessels, and an oily medulla.*

Rokitansky gives as a characteristic of one form of mollities ossium (to which he applies the names of "*osteo-malachia*" or "*rhachitismus adultorum*"), that it affects principally the bones of the trunk, those of the extremities being affected in a subordinate degree; that it occurs especially in childbed women, and is often associated with cancer of the internal organs. This eminent pathologist also states that, in this disease, the bony corpuscles (*lacunæ*) are found empty, and without *canaliculi*; that the lamellar structure is also lost, and the structure satured with fat. The extract obtained by boiling differs, both from chondrine and from the normal animal matter of bone, a circumstance which he considers to be the most remarkable characteristic of the disease. He states further, that this form of the disease is painful, malignant, and has never been cured. In some cases, the muscles were in a state of fatty degeneration.

Mr. Dalrymple concludes, from microscopical observations of one variety of mollities ossium, that it was a simple fungoid, *malignant* condition of bone. He found the areolar spaces enlarged by the absorption of their partitions, and great increase in the vascularity of the lining membrane. The "lacunæ" were also enlarged, and the "canaliculi" considerably shortened, in the parts most affected. The red, grumous matter contained in the cavities, exhibited a large quantity of blood corpuscles, together with numerous nucleated and nuclear cells, with many cytoblasts, and some few caudate cells. Many oil globules and fat cells were also present. He considers the disease to differ from malignant osteo-sarcoma, in there being no deposit of new bone, and that the caudate cells, instead of increasing, become disintegrated, resolved into granular matter and oil globules, and finally dissolved.*

Professor Paget considers, that there are two kinds of mollities ossium, in one of which he places the *Rhachitismus adultorum*, described by Rokitansky, as well as that just quoted from Mr. Dalrymple, where the bones are reduced to a soft, flexible and cartilaginous condition simply. In the other variety, which he considers to result, like *fragilitas ossium*, from *fatty degeneration* of bone, he would place all the cases which have occurred in this country, including that of Mr. Solly's before described. Of the former variety, this pathologist has never seen a specimen, and he does not, apparently, consider it either a malignant or a frequent condition of the bones. His observations have led him to conclude that the grumous contents of the bony cylinder in this disease, of whatever hue—yellow, pink, crimson or dark red — are composed of disguised fat. In part of a femur presented to the Hunterian Museum by Mr. Tamplin, he found free oil globules in large quantity, fat cells filled with oil, or empty, collapsed, and rolled up, and crystals of margarine contained in or without the fat cells. The colour, which was yellow, pink and crimson, was owing to the hue of the oil globules, nuclei and granules of the collapsed fat cells. There was no excess of blood corpuscles whatever. In a portion of a femur presented by Mr. Howship, there was left, after boiling, only a small quantity of white crystalline matter.†

John Hunter remarked, in a case of mollities ossium, described by Goodwin in the *Med. Observ. and Inquiries*, that the bony structures were spongy, deprived of their earthy matter, and so soaked in soft fat as to resemble a fatty tumour.

In the pelvic bones of a female past the middle age, affected with the *rostrated* variety of *angular* deformity, I found, on making sections, a large quantity of a yellowish fatty matter contained in the areolar structure. This was particularly the case, also, in the head and neck of the femur, which even after long maceration, had entirely a smooth and greasy section. On applying heat to various portions of these bones, in order to ascertain the proportion of earthy constituents, they ignited and burnt with a copious bluish, fatty flame, with much smoke, and continued to burn freely till all the fatty matter was exhausted. The bones, which were very light,

* Med. Chir. Trans. vol. xx. p. 360.

* Dub. Jour. vol. ii. 1846.

† Lectures on Nutrition, Med. Gaz., 1847, p. 234.

even before incineration, left, after exposure to a red heat for some time, a very porous and light inorganic structure. The following results were obtained by thus burning off the organic components—100 *grains of bone*,—

	grs.
From the body of an upper lumbar vertebra left—*of earthy matter* - -	31
„ the last lumbar vertebra - -	27
„ lower end of the sacrum - -	24
„ ilium (cotylo-sacral rib) - -	40
„ ischium (near tuberosity) - -	36
„ pubes (near acetabulum) - -	33
„ head of the femur - - -	22
„ neck of the femur - - -	25
„ shaft of the femur (below trochant)	58

When we compare the foregoing proportions of the two constituents of bone with those given by Schreger, as the normal proportions of adult bone — viz., 20·18 animal, and 74·84 earthy matter—the diminution of the inorganic constituents appears very striking, and still greater when compared with those of aged bone ; although less so than in the results of the analysis of Dr. Leeson, in the extreme case recorded by Mr. Solly before given.

The femurs were perfectly normal in shape, as also were the bones of the lower leg, but the pelvis was a *rostrated* one, the superior pubic rami being bent in the middle nearly at right angles, and much deformed and contracted in all its diameters. It was remarkable, that, at the bend of the superior pubic rami, and at the suture of the ischio-pubic rami, there was a complete deficiency of osseous matter, so that after maceration, the pubes separated at these points ; showing that the connection and continuation of the bone in these places was purely ligamentous, or by organic matter, as if resulting from an ununited fracture.

The sudden diminution of the hard constituents in the head and neck of the femur, as compared with its shaft, is worthy of observation in reference to the bending and fracture of the femoral neck in old people.

The smaller proportion of earthy matter in the pubes, as compared with the ilium, and in the sacrum and lumbar vertebræ, as compared with the femoral shaft and pelvis, will account for the greater yielding and deformity which are observed in these parts in the angular pelvic distortion, especially in the rostrated variety, and will be referred to presently in the consideration of the mechanism of pelvic deformities.

In the analysis made by Dr. Bostock of the dorsal vertebræ of a woman affected by mollities, he found, that the proportion of the earthy constituents amounted to only one-fifth of the whole weight in one part of the bone, and to one-eighth only in another ; while in a healthy bone from the same part, they amounted to more than one half the whole weight.*

In the analysis given, in Rokitansky's work before cited, of a portion of bone affected with this disease we find—in 100 parts :

Phosphate of lime and magnesia -	17·48
Carbonate of lime and soluble salts	6·32
Total of inorganic matter	23·80
Cartilage vessels and fat -	76·20

Specific gravity of the bone 0·721.

Among the reasons adduced in favour of the supposition that this disease is sometimes a malignant one, besides the general and violent pains that usually *precede* the deformity, its incurability and unchecked course towards a fatal termination, have been given. That this result is not invariably the case, the following case quoted from Naegele will show, in the fact that the pelvic bones had *regained* their normal hardness. In the pelvis whence the foregoing analysis was taken, the bones had, most probably, at some former period been much softer than they were at the time of death. Such cases also show, that though very frequently, the pelvic bones distorted by mollities are so soft and pliable as to yield, sometimes considerably, to the fœtal head ; yet that this is by no means always the case, nor should it be taken, as it is by some obstetricians, as a characteristic mark of this disease affecting the pelvis.

A very minutely detailed case of pelvic distortion, resulting clearly from one or other kind of *mollities ossium*, is given by Naegele.* The subject of the case, after having borne six children (five healthy, full sized, and living, and the sixth still born), became affected with this disease, which brought about such extensive pelvic distortion and contraction, that, at the seventh labour, the Cæsarian operation was rendered necessary, from the consequences of which the patient died after the fourth day. The shortness of the time in which the pelvis became so much distorted, together with the extent of the deformity, and the fact that, at the time of the patient's decease, it had *regained* its normal hardness, render the case a very remarkable one. Naegele considered it as the most contracted pelvis that had ever come under his observation.

The anterior wall was pushed upwards and the posterior downwards, the superior plane being bent at the acetabula, so that the upper border of the pubic symphysis was level with the upper surface of the 4th lumbar vertebra ; and a line drawn from one anterior superior iliac spine to the other, cut the upper surface of the 3rd lumbar vertebra at its posterior half. The innominate bones were pushed together, and presented the acute furrow, like cracked pasteboard, on their inner surfaces. The sacrum was bent almost double. The measurements are given by the author, as follow †: —

* Med. Chir. Trans. vol. iv.

* Erfahrungen und Abhandlungen; and Appendix to Das Schräg Verengte Becken.

† The measurements used by Naegele, (Rhineland or Prussian,) are very slightly larger than the corresponding English ones.

From the anterior inferior iliac spine, to the opposite point on the iliac crest posteriorly—on the left side, 2 inches 4 lines; on the right side, 2 inches 6 lines. From the apex to the upper surface of the sacrum, 16 lines only; to the junction of the 1st and 2nd sacral pieces, $10\frac{1}{2}$ lines. From the left superior pubic ramus a little internal to the pectineal eminence, to the body of the 4th lumbar vertebra on the same level, *only* $2\frac{1}{2}$ *lines*. Between the same points on the right side, $6\frac{1}{2}$ lines. The sides of the sub-pubic arch were only 3 lines apart, and more contracted near the sciatic tuberosities than above, by these processes being pushed inwards. The pubes in this pelvis, as represented in the drawings given by the author, are bent in the middle of their superior rami, thus producing the rostrated form.

A like case of progressive pelvic deformity from *mollities ossium* is described by Dr. Cooper.* The patient, Elizabeth Foster, had perfectly easy delivery in her three first labours; before the fourth, she had, while pregnant, rheumatic fever, and afterwards constantly suffered from universal pains of a rheumatic character, followed by gradual spinal distortion. From the fourth to the sixth labours, they were increasingly difficult, and in the seventh and eighth she was obliged to be delivered by craniotomy, the sacro-pubic diameter being reduced to 2 inches. Three years after, she again became pregnant, when the sacro-pubic diameter was found to be reduced to $1\frac{1}{4}$ inch, becoming gradually narrower on each side. Cæsarian section was performed, under which she sank. After death, the sub-pubic arch was found to be so much contracted, that the sciatic rami were little more than $\frac{1}{2}$ an inch apart. The pelvis was so soft and spongy, that the finger could be easily pressed into its substance, and at the place of attachment of some of the muscles, the osseous substance was found raised into eminences, as if pulled out.

Eight similar progressive cases were observed by Barlow. One woman, on whom he performed hysterotomy unsuccessfully, had given birth to two children, and afterwards had become lame and bed-ridden for four years. In another case of Cæsarian section, also resulting from malacosteon, the woman had previously borne children, and been delivered by the crotchet. In this instance, the conjugate diameter was reduced to $1\frac{1}{2}$ inch; the right sacro-cotyloid, to $2\frac{1}{4}$; the left, to $1\frac{1}{4}$ inch. The last lumbar vertebra and sacral promontory formed a great tumour-like curve in the pelvic cavity, which he was able to distinguish from an exostosis only by its yielding easily to the pressure of the fingers, which a tumour of that nature would not do.† Other cases of this progressive kind have been before alluded to.

The question as to whether the *rickety* pelvis ever assumes the *angular* or *cordiform* shape, is one which has occupied considerably the attention of many obstetricians.

* Med. Observations and Inquiries, vol. v.

† Essays, p. 355.

It was very ingeniously advocated by Dr. Hull in his Letters to Symmonds, and laid down by the younger Stein and others on the Continent, that the ovate form of pelvic distortion with contraction of the diameters of the inlet and enlargement of those of the outlet of the pelvis, was the characteristic and invariable form of rickety disease; as that of the angular cordiform shape, with contraction of both outlets, was of *malacosteon;* and the opinion seems to be still frequently held by obstetricians both abroad and in this country.

Dr. Murphy considers that, though the oval pelvis is not the necessary consequence of rickets, nor the cordiform of *mollities ossium*, yet that "of necessity, the softened adult pelvis would take the shape called cordiform, while the infant pelvis would be transversely lengthened;"—unless in the infant, "the spine be softened and bent as well as the pelvis," so as to throw the weight of the body more upon the pelvic cavity, as by a "*backward* curvature" such as he has figured, in which cases he supposes that angular deformity takes place in the child.* This conclusion he draws from the hypothesis that in the child, because of the straightness of the spine, a line passing through the centre of gravity, and consequently the weight of the spine, would fall altogether *in advance* of the pelvic cavity, and that consequently the acetabula would be pressed up behind it, and of necessity, *diverge*, because of the sacrum pressing down between them; while, in the adult, the weight of the body falls within the pelvis and between the acetabula, which consequently would be pressed inwards towards it. In considering the mechanism of these pelvic deformities we shall again have occasion to refer to this explanation. But this author also thinks that a condition of bones identical with or allied to rickets, may be induced in young adult females, whose health is depreciated, and powers of nutrition impaired, by the confined or unhealthy nature of their employment; and that there is thus constituted a special kind of mollities ossium, a *rickets* of *adults*, in which cases the pelvis will assume the cordiform shape. The frequent occurrence of spinal deformities at this age, is an evidence of a deficiency in the supply of osseous material.

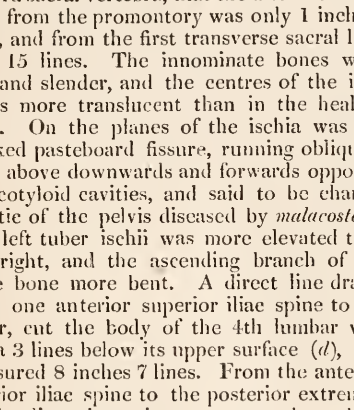
Naegele, who warmly combats the opinion that the infant rickety pelvis is always elliptical, quotes in support of his arguments against it, a case attended by Dr. J. A. Beyerle and Professor Fischer, of Mannheim. The history of the case, and the appearance of the patient herself, and of her father, brothers, and sister, indicated scrofula and extensive rickety deformity existing in the family. The patient had been deformed from the earliest youth, and had not attempted to walk or stand till she was seven years old. She was of very small stature,—4 feet 3 inches, had a projecting sternum, an awkward, shambling, waddling gait, and a remark-

* Lectures on Parturition, p. 32.

able projection of the abdomen, caused by a great increase in the normal forward bend of the lumbar curve; with an equivalent projection of the sacrum posteriorly, from the horizontal position of that bone; so that the plane of the superior pelvic opening was, in the upright position, completely vertical. The lower extremities were not, however, deformed, neither the bones of the upper nor lower leg being bent. About the age of thirty, she became pregant, and died after the necessary performance of the Cæsarian section.

On being examined, the lumbar vertebræ were found much curved forwards, and small, slender, and weak. The sacrum was placed nearly horizontal from before backwards, its posterior part projecting very much behind (see *fig.* 120. *a*). It was sunk so much between the ilia that the centre of the 4th lumbar vertebra was opposite to the upper border of the pubic symphysis, and was bent so much about the 3rd sacral vertebra, that the distance of the apex from the promontory was only 1 inch 9½ lines, and from the first transverse sacral line, only 15 lines. The innominate bones were thin and slender, and the centres of the iliac wings more translucent than in the healthy bone. On the planes of the ischia was the cracked pasteboard fissure, running obliquely from above downwards and forwards opposite the cotyloid cavities, and said to be characteristic of the pelvis diseased by *malacosteon*. The left tuber ischii was more elevated than the right, and the ascending branch of the same bone more bent. A direct line drawn from one anterior superior iliac spine to the other, cut the body of the 4th lumbar vertebra 3 lines below its upper surface (*d*), and measured 8 inches 7 lines. From the anterior inferior iliac spine to the posterior extremity of the linea innominata, measured on both sides, 2 inches. From the ischial tuberosity

Fig. 120.



Angular rickety pelvis. (After Naegele.)

to the most elevated portion of the iliac crest, measured on the right side, 6 inches, on the left, 5 inches 7 lines. From the tuber ischii to the pectineal eminence, measured on the right side, 3 inches; on the left, 2 inches 11 lines. The height of the pubic symphysis was 18 lines.

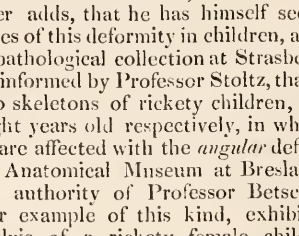
The *superior opening* was angular, with an acute and somewhat symmetrical curve of the cotylo-sacral ribs on each side, and a gradual and equable curve inwards at the union of the ilium and superior pubic rami *at the acetabula* (*b*), which brings the body or acetabular portion of the pubis, to within 5 lines of the body of the 4th lumbar vertebra, the under surface of which is on the same level; the same measurement on the left side being 6½ lines. The distance from the anterior and lower border of the same vertebra to the upper border of the pubic symphysis, was 1 in. 1 line; and from one superior branch of the pubis to the other near the acetabula, 1 in. 7 lines. The pubis presented the usual outward bend at the spines on each side of the symphysis (*c*).—At the *inferior opening*, the distance between the ischial tuberosities was 1 in. 5½ lines only; and the nearest approximation of the ascending branches, 1 in. 1 line.

The shape of this pelvis, of which the author gives three lithographic sketches, had caused it to be frequently mistaken for the results of *mollities ossium*, but the appearance of the bones in texture, lightness, and slenderness, &c., was truly rickety, and with the history of the case, gave no reason whatever for the supposition that malacosteon had ever been present or supervened.

In addition to this case, the same eminent observer adds, that he has himself seen two examples of this deformity in children, and that in the pathological collection at Strasbourg, as he was informed by Professor Stoltz, that there are two skeletons of rickety children, of one and eight years old respectively, in which the pelves are affected with the *angular* deformity. In the Anatomical Museum at Breslau, also, on the authority of Professor Betschler, is another example of this kind, exhibited by the pelvis of a rickety female child aged ten years. Many other similar examples are given by Burns, Otto, Wallach, and Krumbolz. Rokitansky also found the angular deformity in rickety pelves, but in a minor degree of distortion.*

In the Museum of King's College, London, are two rickety pelves of children of about from four to six years old, both of which are affected with angular deformity of the pelvis.

Fig. 121.



Angular child's pelvis from rickets.

A drawing of one of these is given in figure 121. In the larger of the two, the curves of the femurs and leg bones are bent di-

* Pathological Anatomy: Pelvic Abnormalities.

rectly forwards, without any lateral deviation inwards or outwards. In the Hunterian Museum also, there is a rickety skeleton of a child of six years, in which the pelvis presents the angular deformity and approximation of the acetabula. In none of these specimens is there any great backward curvature of the spinal column, though, in the last instance, the sacrum is bent so much forward, that the tip of the coccyx is almost on a level with the superior plane in the centre of the opening.

It is, however, especially remarkable that in *all* these last-mentioned specimens, as well as in that figured by Naegele and just described, the angle of the bend or *culm* of the *lateral curve* produced by the pressure inwards of the heads of the femurs, takes place *in the acetabula* at the line of junction of the two upper pieces of the innominatum, and not in the superior branch of the pubis itself, as in most of the cases resulting from *mollities ossium.* This is evidently produced by the more facile and greater yielding of the as yet unossified cotyloid cartilage, rendered softer and more tardy in ossifying, by the effect of the disease upon its nutrition.

That such a yielding does take place in this cartilage from disease and pressure is shown still more strikingly in another case in the Hunterian Museum (No. 3423.), in which it has bent *outwards*, instead of inwards, and thus is produced an elliptical distortion of the pelvis. This skeleton is from a young subject, in which the pelvic bones had not yet become soldered together. The head and neck of the left femur are nearly destroyed by caries, which doubtless also extends to the acetabulum itself. Both the femurs are extremely flexed and adducted on the pelvis, and seem, especially on the diseased side, to have, by the constancy of this position, pushed upwards and backwards the pubis, so as to cause a distinct bend at the cartilaginous cotyloid line of junction, and an elevation of the pubic symphysis. By this means, the acetabula are pushed outwards, and the superior pelvic opening assumes an elliptical shape; though the cotylo-sacral arch is but slightly spread out, and the ischial tuberosities are normally placed. The lumbar curve and sacral promonotory deviate slightly towards the left side, and the bones are remarkably small and light, showing the prevalence of the rickety tendency.

From these cases, it seems reasonable to draw the conclusion, that the softened infant pelvis does in a great many cases assume the cordiform shape, and that without any *backward* spinal curvature; but, on the contrary, the case quoted by Naegele shows that it is co-existent with excessive *forward* curvature of the lumbar spine, such as would throw the weight of the body entirely in front of the vertically placed pelvic brim; and thus, according to Dr. Murphy's view, of necessity, produce the ovate and not the angular deformity.

We may also conclude that when, by mechanical causes, the *angular* shape is impressed upon the softened infant pelvis, it will yield most readily and extensively at its weakest point — viz. the still cartilaginous line of ilio-pubic junction *in the acetabulum;* and that, as in the instances now given, and indeed in all that I have myself examined, the shape of the angular pelvis resulting from *rickets* in infancy is never *rostrated*, in the sense to which that expression is confined in the present article; but, that this form is usually seen only in the angularly deformed pelvis resulting from the *mollities ossium* of adults, and commencing after the pelvis has attained its adult development and consolidation, when the bend most commonly takes place in the centre of the superior pubic ramus, which, in thickness, and, in some diseased conditions, as the analysis before given shows, in composition also, is the weakest point of the pelvic circle in the adult. This will, I think, be found a general and useful distinguishing mark between the angular pelvis resulting from rickets, and that of the adult *mollities ossium.*

Whether, on the other hand, the adult pelvis, softened by *mollities ossium*, or the rickets of adults, ever assumes the ovate form of distortion, is a question of supposition merely. I have not been able to find any recorded cases of such a result, though there is no evident reason why this should not occur, under certain mechanical conditions. Rokitansky found that the ovate and hour-glass distortions are, almost without exception, the result of infantile rickets.

Mechanism of the preceding Pelvic Distortions.— In considering the forces which operate in producing the two principal varieties of pelvic distortion previously treated of, it is necessary carefully to separate those resulting from mechanical position, from those which arise from muscular action alone. In considering the former, it will be necessary as carefully to separate the idea of the *line of gravity*— i. e. a perpendicular line let fall from the centre of gravity— from that of the *line of pressure*, which must necessarily pass through the osseous supporting structures, whatever disposition they may have.

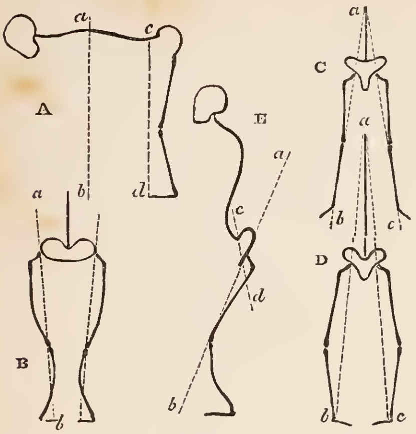
The *centre of gravity* of the *trunk* itself is that which influences most considerably the form of the softened pelvis in the sitting as well as the upright position. This is placed by Weber in the transverse vertical plane of the spinal column, which here falls considerably in front of the vertebræ, in the thoracic cavity, at the level of the sterno-xiphoid articulation (see *fig.* 122. A, *a*).

In the most easy standing position, this centre of gravity is placed directly above *that of the whole body*, at the sacro-lumbar articulation (A, *c*); so that perpendicular lines let fall from each to the ground will exactly coincide, and (in the well-made subject, after passing through the sacral promontory and the acetabula) fall between the feet as the basis of support. In the sitting posture, it falls a little posterior, between the ischial tuberosities.

To preserve the standing posture, it is

necessary that the line of gravity of the whole body—viz. that from the lower centre—should

Fig. 122.



A. Diagram of the lines and centres of gravity of the trunk, *a b*; and of the whole body, *c d*.

B. Outline of the lines of pressure in the pelvis and legs in the *ovate rickety* distortion, during the standing posture.—*a b* lines of direction of the pressure of the heads of the femurs in the acetabula,—upwards and *outwards*.

C. Outline of the pelvis and legs in the *angular rostrated* pelvis of the *adult*, resulting from *mollities ossium*. *a b*, *a c*, direction of pressure in the acetabula when the legs are not deformed,—upwards and *inwards*.

D. A similar outline in the *angular rickety* pelvis of the *child*, when the legs are bent *outwards*,—direction of pressure *inwards*.

E. Outline of abnormal antero-posterior curves of the spine, pelvis, and legs. *a b*, direction of the pressure in the acetabula *backwards* increased by the forward curve of the femora. *c d*, line of traction of the psoas muscles increasing the deformity of the pelvis.

fall anywhere between the extent of longitude of the feet (*c d*).

If the trunk, however, bend forward, its centre and line of gravity is advanced beyond that of the whole body, and a share of the support of the trunk, equivalent to the degree of distance of these two lines (*b*, *d*), falls upon the muscles and ligaments of the posterior part of the spine, and a corresponding strain upon their attachments to the sacrum and posterior part of the pelvis. This instance may be taken as an example of many others, in which the mechanical position of the line of gravity influences muscular action, the effects of both falling upon the lines of pressure and support in the pelvis.

For the preservation of the sitting position, it is only necessary that the line of gravity of the trunk (*a b*) should fall within the extent of the basis of support, which is, from more or less of the whole extent of the hams in front to the ischial tuberosities behind. Hence the greater facility with which a person sitting down is pushed backward than forward.

The *line of pressure*, on the other hand, passing down the centre of the bodies of the vertebræ will, in the well-made subject, when standing on both legs or sitting, divide at the sacral promontory, into two equal parts, each of which traverses, first the lateral sacral masses to the sacro-iliac joint; from this point, in the *upright* position, it passes along the cotylo-sacral rib to the heads of the femurs, describing in its course the C-like curve. In the *sitting* posture, it passes down the ischio-sacral buttress to the tuberosities. It will be borne in mind that each of these standing and sitting arches has its tie, which prevents it equally from starting *outwards* or pressing *inwards* at the extremities; that for the cotylo-sacral arch being the united superior pubic rami, and that for the ischio-sacral arch, the united ischio-pubic rami. The cotylo-sacral arch and its pubic tie, united at the acetabula, and placed in the same plane, form in man, as we have seen, a lateral arch made up of the two halves, which supports on its culm the inward pressure of the head of the femur. The cotylo-sacral portion also sustains, in addition, its upward and backward pressure.

The first effect of the softening of the osseous supports in this line of pressure is to increase the natural curves which occur in it. Thus we see an increase in the dorsal, lumbar, and sacral curves, in the cotylo-sacral, femoral, and tibial (*fig.* 122. E). The next effect is to produce lateral curves, which present generally their concavities towards the line of gravity, and are always associated with *compensating curves*, so as to keep the line of gravity within them, about which they produce a wavy line, as is seen in the deformed spine. When this is not the case, the support of the weight falls more upon the tension of the muscles, and ligaments, and parts of bone on the convex side. In the pelvis, and, to some degree, in the bones of the legs, however, these results are modified by the lateral duplication and division of the lines of pressure; and in the pelvic skeleton this effect is still further increased by the circular union of the lateral structures, and by the pressure or traction of the bones of the legs, conjointly or individually.

The alteration of the position of the centre of gravity of the trunk, by deformity of the spine low down, will also have its effect upon the pelvis, by necessitating a constrained and unnatural position to prevent the body falling. Deformities confined to the upper part of the spine are seldom accompanied by deformed pelvis, owing, probably, to the little effect they have in altering the centre of gravity. In addition to these general changes from mechanical pressure, there is, in this softened state of the bones, the powerful effect of combined muscular action.

The influence of *continued posture* on these changes will be found to be the origin of most of the differences of form we have seen in pelvic distortions. Let us consider the effects of mechanical position and muscular action in the *recumbent*,—*sitting*,—and *standing* positions respectively, on the softened pelvis

In *lying upon the back*, the softened pelvis will have a tendency to become flattened antero-posteriorly, by the sinking of the pubic arch, at the same time that the traction of the femurs and muscles of the lower extremities outwards will tend to separate the acetabula and increase the transverse diameters. This I apprehend to be the commencement of the *elliptical* pelvic deformity, which occurs in the majority of the softened pelves of infants, whose most frequent and long-continued position is the dorsal recumbent. The angles of the pelvis with the spine will also have a tendency in this posture to become *increased* by the weight of the inferior extremities. If the softening be great, and the position long-continued, the symphysis pubis would also sink, producing the *hour-glass* form of pelvis; a disposition which would be increased by the traction of the levator ani and weight of the bladder. There would also be a tendency to flattening of the sacrum. In *lying upon the side*, on the other hand, there is a pressure, through the trochanters, upon the acetabula, which, if long and frequently-accustomed, will cause the lateral pelvic arches to yield and bend inwards at the cotyloid line of junction, in children as yet unossified, and produce the first bend or tendency to the *angular* deformity. The effect of these first impressions are, as Dr. Ramsbotham observes, illustrated by making an elbow in a piece of wire subjected to pressure at each extremity. In the undeveloped pelvis also, the facility with which these impressions are made upon the pubic tie is rendered greater by the greater tardiness of its ossification than in the other innominate pieces. In some instances, pelves seem to have been impressed in this manner on *one side only*, so that the two sides present an approach to the two different varieties of deformity, as will be presently alluded to.

In the *sitting* and *standing* positions, a more powerful distorting influence is brought into play—viz. the pressure of the weight of the body on the softened pelvic arches.

The *sitting posture*, when the *elliptical* form has already been impressed upon the pelvis, will still further tend to separate the acetabula by the starting outwards of the lower extremities of the ischio-sacral arch under the pressure of the weight of the trunk on the sacrum; and thus the separation of the tuberosities, the enlargement of the transverse diameter of the outlet, and the spreading out of the subpubic arch take place. At the same time the sacral promontory sinks into the pelvis under the weight of the trunk, while the lower part of the sacrum is kept forwards by the sciatic ligaments, so that a bend takes place in the middle of the bone. This bend will be still further increased by the divergence of the ischial tuberosities, permitting the weight of the spine to be brought to bear upon the coccyx and lower end of the sacrum and against the sitting surface. The total direction of the pressure on the ischial tuberosities being upwards and backwards, the curve of the ischio-sacral arch (coinciding with that of the cotylo-sacral at the top of the sciatic notch) takes place in that direction, and increases the acuteness of the C-like curve.

These effects upon the sacrum and ilia, and pelvis generally, will be increased by the action of the powerful erector spinæ muscles, and psoas and iliacus muscles, exercised in keeping the trunk erect upon the pelvic lever (see *fig.* 122 E, *e d*). These muscles have, in addition, much influence in shortening the spinal column itself, already bending under the weight of the body, and,—following the general tendency of elongated substances yielding to pressure at both ends to twist laterally,—the lumbar curve and sacral promontory become placed on one side the median line. This tendency, from reasons before explained, is generally to the left. Under the increased inclination of the pelvic angle, the abdominal muscles will tend to draw the flattened pubes upwards still nearer the sacral promontory, diminishing the conjugate diameter. In extreme deformity, the iliac wings are pressed still further outwards and everted by the pressure of the lower ribs resting upon them, as we have observed in one of the detailed examples.

But when the lateral pelvic arches are already impressed with the *angular* deformity, the sitting posture has the effect of merely increasing the inward bend, and approximating the acetabula and sciatic tuberosities to the sacrum, pressed down by the superincumbent weight. Dr. Rigby mentions that frequent riding on horseback at an early age will produce contraction of the inferior outlet, even in the healthy pelvis, and that the females of those American nations who ride much bear few children, and are often three or four days in severe labour.

In certain cases, in which the acetabulum on one side only has been pressed inwards by the constant use of the lateral recumbent position, or in which the centre of gravity of the trunk has been permanently shifted to one side by the spinal bend, a habit is acquired of sitting more upon one ischial tuberosity than the other. This unequal pressure produces inequality of distortion, and presses the tuberosity and acetabulum of that side *inwards*, while the opposite one presents the usual *divergence* of the elliptical distortion. This effect is also contributed to in like manner, under the same circumstances, in the standing position, by the pressure being greater and more frequent upon one femur than the other; and thus we have produced a sort of oblique deformity, of which I have seen several specimens.

In the Museum of King's College are three skeletons, all presenting more or less a tendency to this peculiar modification of the ovate deformity. In the Hunterian Museum is another, in an adult female skeleton, still more marked.

It is somewhat remarkable that, in all these examples, the trunk is bent towards the right side, and the lumbar curve and sacral projection towards the left; so that the line of gravity, and consequently the greatest share of supporting the weight of the body, falls nearer the left leg and the left side of the pelvis. The effect is such as to produce great similarity in the form of all these pelves, which vary only in the degree of distortion. The sacral promontory is directed to the left side, while the sacral concavity is more or less twisted so as to face the left acetabulum. The innominate bone of the left side is placed lower and more vertical than that of the right side, which appears longer and less bent; so that the left ischial tuberosity projects lower and more vertically than the right, which is everted and directed outwards. The left acetabulum is brought nearer to, and more directly under, the sacral promontory, the cotylo-sacral arch being more curved than the right; while the right sacro-iliac joint and lateral sacral mass are higher, the cotylo-sacral curve more open, the iliac wing more spread, and directed, like the acetabulum, more forwards, and the ischio-pubic ramus placed more obliquely, than those on the left side.

In the female Hunterian skeleton, the obliquity of the spine and pelvis are so great, that the upper dorsal vertebræ are placed above the right sacro-iliac joint. The femora are shortened, and curved forwards and outwards, and the leg bones forwards and inwards, in compensating curves. The left knee, however, is more under the line of gravity than the right. A tendency to a somewhat similar twist is seen in an adult hydrocephalic skeleton in the same collection.

These pelves present, at first sight, some resemblance to the very different "*obliquely ovate*" pelvis of Naegele. The most characteristic differences are, the presence of other rickety appearances, and the want of the coincidence of lateral deviation of the pubic symphysis with the sacro-iliac ankylosis and malformation of the latter.

Rokitansky includes all the pelves which present a want of symmetry at the sides under the general term of *oblique pelves*, after Osiander's classification, in which he comprehends by far the greatest number of pelvic deformities of all kinds. He gives, as a characteristic of this class,—approximation of the sacral promontory to the pectineal eminence on one side, which side has also a higher level and a less pelvic inclination than the opposite one, originating in a lateral curve and torsion of the sacrum towards the contracted side, —and straightening out of the linea innominata on the opposite side, between the sacro-iliac joint and the acetabulum. It includes the frequent pelvic deviations resulting from lateral curvature of the spine, but most frequently arises from rickets, or displacement of the femur by hip-joint disease or violence.

To a rickety child, who rarely begins to walk till after the usual age, by far the most frequent positions are the two which we have just considered, and the mechanism of these positions, in my own estimation, is quite sufficient to account for the first impression of the most frequent deformity of the rickety pelvis, the *ovate*, as well as for the not uncommon *angular* infantile distortion.

In *standing* and *walking* the supporting pressure on the pelvic structures is sustained, either divided or alternately undivided, between the cotyloid cavities and the sacrum. From the peculiar disposition of the cotyloid articulation, the pressure of the head of the femur is exerted in two directions, 1st, upward and backwards along the cotylo-sacral rib, which is the principal line of pressure, and, 2nd, inwards on the lateral pelvic arch. In the upright position the softened cotylo-sacral rib yields in the direction of its C curve, which becomes more acute as the sacrum sinks. An increased obliquity of the pelvic inclination, such as has been stated to be generally consequent upon the advance of the sacral promontory and increased lumbar curve in the elliptical deformity, will bring the line of gravity, both of the trunk and whole body, in *front* of the acetabular supports, which will cause them to increase the backward curve when pressure is exerted upon them (see *fig.* 122. E, *a b.*), But that such a condition is produced by a greater obliquity of the *normal* infant pelvis than that of the adult, or that this alone is sufficient to account for the elliptical deformity taking place usually in the infant pelvis, by causing divergence of the acetabula under pressure during the upright posture, as asserted by Dr. Murphy, is a conclusion which the results of the observations given in a former section, as well as those of Weber, therein stated, will not at all admit of;—for, as was there seen, the obliquity of the normal infant pelvis is not at all greater, if as great, as that of the adult.

But if the acetabula are already separated by the *elliptical* deformity, or if the leg bones yield *inwards*, so that the pressure on the acetabular articular surface at its upper vaulted part is directed *upwards* and *outwards*, as seen in the accompanying diagram (*fig.* 122. B, *a*, *b*), then the pressure *inwards* of the heads of the femurs upon the lateral pelvic arches is taken off, there is traction instead of pressure on the pubic *tie*, the acetabula become still more widely separated, and the elliptical deformity increased. In such specimens of ovate pelvic deformity as have the leg bones attached, I have found the tibiæ and fibulæ bent much inwards, or the leg bones so disposed by an *inward knee-bend* as to take off the *inward* pressure at the acetabula, and even sometimes by extreme adduction of the femurs, so as to exercise a strain upon the round ligaments of the hip joint and rotator muscles, and thus produce a direct *outward* traction. In this position of the bones, the action of the adult muscles which support the erect posture—viz., the great glutei and psoæ, will be such as to increase the deformity (see *fig.* 122. E, *c d*), as well as those before mentioned which sustain the spine erect.

If the *angular* deformity have been already impressed upon the infant pelvis by the bending of the cartilaginous junction, while the bones of the legs, and in some degree those of the pelvis, retain a sufficient degree of hardness to resist the bending, then the *inward* pressure of the heads of the femurs remains in its full force, associated with the *upward* and *backward* pressure, and the deformity is increased by the upright position (*fig.* 122. C, *a b*, *a c*). The same result is also produced in an increased degree, if the leg bones yield outwards, so as to direct the pressure of the heads of the thigh bones more towards the median line. This will be better understood by referring to the diagram (*fig.* 122. D, *a b*, *a c*).

Naegele observes, that when the lower extremities are curved and distorted the pelvis will generally be deformed; and that such a condition more especially, or where one hip is higher than the other, with an unsteady gait, a projecting abdomen and lower jaw, and retraction of the arms and thorax, diminutive stature, &c., should lead the accoucheur to suspect deformed pelvis.*

The adult pelvis, softened by malacosteon, appears to undergo greater distortion than is proportionate to that of the leg bones. In that upon which the experiments before mentioned, to ascertain the proportions of the osseous constituents, were performed, the bones of the lower extremities were almost entirely symmetrical and well formed, and the proportion of earthy matter contained in the femurs much greater than in the pelvic bones, especially in the pubes (at one point of which it was entirely deficient) and the sacrum. The pubes, as they are also the thinnest pieces of the innominate bones and sustain a great amount of the inward pressure, which exists, in these cases, to its full extent, seem to be the first to give way in the more complete and rapid softening of "*mollities ossium adultorum*." The consequence is, the approximation of the acetabular extremities, and increased curve of the cotylo-sacral arch, so as almost to touch the sunken sacral key-stone; and the starting forward and upwards of the crown of the pubic counter-arch, so as to produce the *rostrated* symphysis.

The muscles before enumerated, which support the erect posture, as they are in the adult more powerful and developed, have a corresponding effect in increasing the contraction of the diameters consequent on the distortion. The bones yield between their contracting distances in the direction already impressed upon them. The acetabula are pressed backward by the psoæ and iliacus muscles, and the ischial tuberosities and trochanters approximated by the pressure of the great glutei, which, aided by the pyriformes, will also draw forward the lower part of the sacrum and coccyx. The powerful influence of the adult muscles upon the pelvic bones partially softened, and especially that of the great glutei upon those bounding the diameters of the inferior outlet, will produce many of the *partial deformities* before treated of, as the influence of mechanical posture in a limited extent, or short duration of the softening disease, will produce others, principally those of the pelvic brim.

* Lehrbuch, § 444.

The peculiar variety of the partial deformity will depend upon the frequency of the use of one particular posture or set of muscles; and this will depend chiefly, in the child, on the concurrent ailments which usually affect it, and in the adult on the nature of his or her habits and employment.

The degree of the backward curvature of the cotylo-sacral arch seems to depend upon the degree of anterior lumbar curvature, which necessitates a forward projection of the femurs to keep the line of gravity between the feet (see *fig.* 122. E, *a b*).

The rostrated pelvis, with *elongated* antero-posterior diameters, apparently results from the coincidence of the softened pubes with the causes of oblong deformity before adverted to, as produced by a *backward* spinal curve, causing the line of gravity to fall considerably *behind* the acetabula, and dragging backwards the superior part of the sacrum.

The mechanism of these important pelvic deformities has been entered into more in detail because of the evident practical inferences which may be drawn from it with regard to the treatment and position of children, especially females, afflicted with rickety disease.

Degree of obstruction. — Pelves affected by the foregoing distortions are usually arranged by British obstetricians, according to the degree of obstruction at the brim, into three classes: —

1st. Those which will suffer the full-sized fœtal head to pass entire.

2nd. Those through which delivery may be accomplished "*per vias naturales*," by means of premature labour, craniotomy, or mutilation of the fœtus.

3rd. Those in which the degree of deformity is so extensive as to call for the Cæsarian section, or the very early induction of abortion.

The limits of the first class have been variously stated by different obstetricians, according to their opinions regarding the obviou variations in size of the fœtal head, and its degree of ossification. The following list conveys the opinions of the most eminent authorities upon the *lowest* limits through which the fœtal head can pass entire: —

	Diameters Conjugate.		Trausverse.
Ramsbotham, Churchill, Lee, and most obstetricians - -	3 ins.	by	4 ins.
Aitken and Osborne - - -	3 „	„	sufficient.
Josh. Clarke - - - - -	3½ „	„	„
Burns, Davis, and Le Roi - -	3¼ „	„	„
Barlow (Essays) - - - -	2¾ „	„	„
Busch (Berlin) - - - -	2½ to 3	„	„
Ritgen - - - - - -	2	„	„

The lowest limits of the second class of pelves involves a great difference of opinion as to the lowest space required for the safe performance of craniotomy: —

	Conjugate.		Transverse.
Ramsbotham - - - - -	1⅜ ins. or	by	3½ ins.
Osborne, Hamilton, and Gardien -	1½ „	„	3 „
Davis and Barlow - - -	1½ „	„	1½ at inf. outlet.
Baudelocque - - - -	1⅔ „	„	„
Burns, Hull, and Churchill -	1¾ „	„	„
Dewees - - - - -	2 „	„	3½ ins.

In these cases, according to Ramsbotham, it is rare that the transverse diameter does not exceed three inches. Less room is required if the brim alone be distorted, according to the same author.

All pelves contracted in their diameters below the measurements given in the last list may undoubtedly be considered to require, for the delivery of a fœtus of viable or full-grown size, the abdominal section.

Dr. Robert Lee, however, advocates strongly, and with great justice, the propriety of inducing abortion in these deplorable cases, as a means of saving the life of the mother. When the sacro-pubic diameter is below 1½ inch at the brim, this author considers that abortion should be induced before the fifth month. According to Ritgen, labour should be induced in the twenty-ninth week, when the sacro-pubic diameter is 2 inches 7 lines; in the thirtieth week, when it is 2 inches 8 lines; in the thirty-first, when 2 inches 9 lines; in the thirty-fifth, when 2 inches 10 lines; in the thirty-sixth, when 2 inches 11 lines; and in the thirty-seventh, when exactly 3 inches. When above 3 inches, the case should be left to nature. Barlow thinks that premature labour should be induced when this diameter is contracted to 2½ or 2¾ inches.*

But in many cases, especially on the Continent, a much less degree of contraction of the conjugate diameter has been thought sufficient to justify the Cæsarian operation. In a table given by Velpeau†, out of sixty-two cases where narrowness of the conjugate diameter was the reason adduced for adopting this operation, in one case it was 1 inch only; in eight cases, 1½ inch; in twenty-three cases, 1½ to 2 inches; in twenty-five cases, 2 to 2½ inches; and in five cases, 2½ to 2¾ inches. These, without doubt, include many which the British practitioner would place in the first of the foregoing classes, and were adopted with a view of saving the child's life, at an additional risk to the mother.

The "pelvis oblique ovata," or obliquely contracted pelvis. — This form of pelvic distortion was first distinguished and accurately described by Naegele, the distinguished Professor of Midwifery at Heidelberg, as possessing the following characteristics (*see fig.* 123.): —

1. Complete ankylosis of one of the sacro-iliac joints, with coalescence of the sacrum and ilium, generally leaving no cicatrix nor line of junction.—2. Arrest of development, contraction of the lateral mass, and diminution of the foramina, on the ankylosed side of the sacrum. —3. Narrowing of the innominate bone of the same side, shortening and also flattening of the linea innominata, contraction of the sacro-sciatic notch by the ankylosis, and contraction of the lateral parts of the sacrum and ilium composing the sacro-iliac junction. —4. Shifting of the sacrum towards the ankylosed side, and twisting of its anterior surface in the same direction, together with removal of the pubic symphysis towards the opposite side, so as to be no longer placed in the median line opposite to the sacral promontory, but obliquely directed towards it; a direct forward line from the promontory falling on the superior pubic ramus, between the symphysis and acetabulum, its distance from the former varying with the degree of distortion. The bodies of the lower lumbar vertebræ are also, more or less, turned towards the ankylosed side.—5 On the ankylosed side, the inner wall of the pelvis, both before and behind, is less excavated and flatter than in the normal pelvis. —6. On the side free from ankylosis also, the form deviates from the normal shape, although at first sight it appears healthy. On placing together the corresponding non-ankylosed sides of two of these pelves, separated at the symphysis and in the median line, in which the right and left sacro-iliac joints respectively were ankylosed, Naegele found the pubic bones widely divergent from each other. So that, on this side also, these pelves are abnormal, not only in direction, but in form also, being curved less behind and more in front, than in the normal pelvis. — 7. From this it follows, that the obliquely deformed pelvis is contracted in the diameter which extends from the normal sacro-iliac joint to the opposite acetabulum; while it is *not* contracted, but sometimes, according to the degree of distortion, even widened in the diameter, from the ankylosed joint to the acetabulum of its opposite side. The superior pelvic aperture thus presents the appearance of an *oblique oval* (or oblong), the longest diameter of which corresponds to one of the oblique pelvic diameters, and the shortest to the other oblique diameter. From this appearance of the brim he was led to apply the name above given. That the sacro-cotyloid distance, and also that between the apex of the sacrum and the sciatic spine, is smaller on the ankylosed side than on the other. That the distances between the sciatic tuberosity of the ankylosed side, and the posterior superior iliac spine of the opposite side, and also between the last lumbar spine and the anterior superior iliac spine of the ankylosed side, are less than the like measurements on the opposite side. That the distance between the lower border of the pubic symphysis and the posterior superior iliac spine, is greater on the ankylosed side than on the other. That the walls of the pelvic cavity converge towards the outlet in some degree in an oblique direction, and the sub-pubic arch is more or less narrowed, and turned towards the thigh of the ankylosed side. That the contraction of the sacro-sciatic notch, and the approximation of the sciatic spines, is proportionate to the degree of distortion. And, lastly, that the acetabulum of the ankylosed side is directed more forward than normal, and the opposite one almost directly outward. In most cases, the sciatic tuberosity, and the acetabulum of the ankylosed side, were more elevated than the

* Essays, p. 354.
† Traité des Accouchements, p. 457.

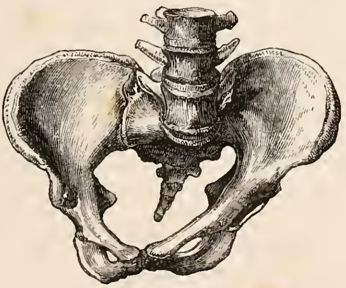
opposing ones; the ankylosed innominate bone appearing as if pushed upwards.

A remarkable peculiarity of this deformity is, that, with the exception of the difference in the side where the ankylosis had taken place, the pelves affected with it were extremely like each other. The strength, texture, and appearance of the bones were perfectly healthy; there was no limping gait observed in the patients affected with it; nor any history of accident, rickets, or malacosteon.

Examples. — Naegele collected, with incredible industry, notes of thirty-five examples of this disease in female pelves, and two in male pelves. Of these, two (one male and the other female) were in the collection of Professor Montgomery, of Dublin, and the others in the various collections of France, Germany, and Italy.

In one case, which was observed during life by the author himself, he observed a slight halt in the gait of the patient, who otherwise was apparently well-built, healthy, and active. In her first labour, at the age of eighteen years, the fœtal head in the early stage was found placed very high, and easily moveable, and the sacral promontory could not be reached by the finger. The patient was delivered, on the third day, with extreme difficulty by the aid of the forceps, and died fifteen days afterwards from puerperal fever. The pelvis was found affected with the oblique deformity, but in strength, weight, and texture perfectly healthy (*fig.* 123.). The sacrum was

Fig. 123.



Pelvis obliquè ovata. (*After Naegele.*)

composed of four pieces only, and measured in length 2 inches 11 lines. The coccyx had six pieces, and measured 1 inch 10 lines. The left sacro-iliac joint was ankylosed, and the same side of the sacrum was shrunk and contracted, so as to measure from the sacral promontory to the usual position of the sacro-iliac joint, only 1 inch 4 lines; whereas the same measurement on the right side amounted to 2 inches 2 lines. The length of the left iliac crest was 3 lines less than that of the right. From the sacral promontory to the left superior anterior iliac spine measured only 3 inches 11½ lines. The same measurement on the right side amounted to 5 inches 4 lines. At the *brim* of the pelvis the measurements were:—

	in.	lines.
From the sacral promontory to the upper border of the obliquely placed symphysis pubis - - - -	3	9
Left oblique diameter -	4	7
Right, ditto, ditto - -	3	5
From the sacral promontory to left acetabulum - -	1	10
From ditto to right acetabulum	3	6

A direct line drawn forward from the sacral promontory cut the left pubis at the junction of its superior and inferior branches, an inch external to the centre of the pubic symphysis. In the pelvic *cavity* the measurements were:—

	in.	lines.
From the centre of the sacrum, to that of pubic symphysis -	4	4
Between the cotyloid walls -	3	11
„ „ ischial spines -	2	11½

At the *outlet*, the measurements were:—

	in.	lines.
Between the sciatic tuberosities	3	0
„ lower border of the pubic symphysis and apex of sacrum	4	4

The lowest oblique diameter in these pelves described by Naegele, was found in one in the Museum of the Hospital of St. Catherine at Milan, in which the left oblique diameter was 2 inches 10 lines only; while the right was 4 inches 6 lines. In the same pelvis, the right sacro-cotyloid measured only 1 inch 8 lines; and the left 3 inches 1 line. In one case, the left, and, in another, the right sacro-cotyloid diameter, was as low as 1 inch 6 lines. In one instance, the distance between the tip of the coccyx and the tuber ischii of the ankyloid side, was only 1 inch. The left side was the one most frequently affected by the ankylosis, but the right side was also found affected in many of the specimens, and, among others, in the pelvis of an Egyptian female mummy.

In addition to the foregoing, three female pelves are described by the same author, in which the oblique deformity was present, but the diminution of the diameters not so great as to produce any great obstacle to parturition.

One of these is in the Museum of St. Bartholomew's Hospital, and is rather above the medium size. The right side of the sacrum is imperfectly developed. The left oblique diameter is nearly 11 lines less than the right; and the right sacro-cotyloid distance, 10½ lines less than the left. A line drawn directly forward from the sacral promontory cuts the right pubis 1 inch external to the centre of the symphysis; and the distance from the sacral promontory to the symphysis is 4 inches 10½ lines. One of them, in Naegele's own collection has six instead of five sacral pieces.

In none of these three pelves, however, is there ankylosis of either of the sacro-iliac joints, although the imperfect development of one side of the sacrum is evident.

In a male pelvis, on the contrary, there was ankylosis of the right sacro-iliac joint, but no atrophy of that side of the sacrum, though the oblique deviation was present in a small degree, the right innominate bone being a little more elevated, contracted, and flattened than the left. The whole appearance of this pelvis bore somewhat a resemblance to that of an animal, and presented on the posterior part of the external surface of each iliac wing a remarkable protuberant growth of bone, as well as an articulation by fibro-cartilage between the left lateral mass of the sacrum and the transverse process of the last lumbar vertebra, which was unusually large.* This last peculiarity was also observed in an obliquely deformed female pelvis in which both the last transverse processes were enlarged and bifurcated; the right being articulated by fibro-cartilage to the corresponding lateral mass of the sacrum, and the left (the side on which the sacro-iliac coalescence existed) similarly articulated to the inner surface of the ilium just above the sacro-iliac junction.†

As a contrast to specimens like the two last, Naegele mentions a well-built female pelvis, in which the left lateral mass or side-piece of the sacrum was, by arrest of development, diminished to the size and appearance of the last lumbar transverse process, but presenting an osseous protuberance, about the size of a bean, as if of the aborted ossific centre, while that on the right side was quite normal in size and appearance.‡

He had seen two others similarly deformed, and mentioned examples in the collections of Sebastian at Groningen, and Vrolik at Amsterdam, and many more in the Pathological Museum at Paris, and others mentioned by Creve and Retzius. Such irregularities of the sacrum are not uncommonly found.

A young female pelvis is described by Dr. Knox § as presenting an example of the obliquely deformed pelvis in an earlier stage. The right half of the sacrum is more than half an inch narrower than the left, the first piece not ossified to the second, and the corresponding half of the pelvic inlet proportionably smaller, the pubic symphysis being opposite the right sacral foramina; but the iliac portion of the innominate bone is tolerably symmetrical, and there is *no* sacro-iliac ankylosis. The lumbar vertebræ present an extensive lateral curve. The same author also mentions that in Dr. Campbell's Museum there is a complete specimen of the obliquely ovate pelvis, deformed on the left side, and presenting a large exostosis on the last lumbar vertebra. In his own possession he has portions of two other pelves, both exhibiting ankylosis of the sacro-iliac joint on the left side, but in one partial only, with twisting of the sacrum and contraction of the ilium, such as would produce, if the specimens were entire, the oblique deformity of M. Naegele. On looking over a collection of human bones taken from an old London graveyard, I have lately met with a well-marked specimen of this disease on the right side, in which there is a line or cicatrix at the sacro-iliac point of coalescence.

From the many specimens which had come under his observation in so short a time, and with but few opportunities of seeing them, Naegele was led to conclude that this deformity occurred pretty frequently.

Its *influence* upon parturition will present an obstacle, not only to the forward progress of the fœtal head, but also to its proper rotation, which will vary with the general extent of the pelvic diameters. If the pelvis be of large size, this deformity, though great, will have less influence than in a smaller pelvis, with a less degree of distortion. The fœtal head may enter the brim with its long diameter in the long oblique diameter of the distorted pelvis; but when in the pelvic cavity it will not be able to make the requisite turn into the antero-posterior diameter of the outlet, and will generally, in the opinion of Naegele, require the use of the forceps to extract it.

The obstruction occurs in the first labours, and its importance may be considered as equal to those resulting from rickets and malacosteon, when it is considered, that in all the cases of labour hitherto published, where this deformity has been present, both mother and child have been lost, although in the hands of the most experienced accoucheurs.

The *diagnosis* of the oblique distortion by the usual measurements is very difficult. It is rendered still more difficult by the absence of any history or peculiar appearance of the patient, indicative of the condition of the pelvis; persons affected with it being usually, in other respects, well built and healthy. The diagnosis, moreover, is usually called for in first labours. The promontory of the sacrum is not to be felt by the finger, an usual indication of plenty of room at the brim; and yet there may be sufficient contraction in the oblique or sacro-cotyloid diameters, to require the Cæsarian section. The antero-posterior diameter, which would show, if a section were made in the centres of the sacral-promontory and pubic symphysis, a clear space of 3½ to 4 inches, may appear, in the living subject, to be contracted to 2½ inches. The contraction of this distortion is as totally unrecognisable by the use of Baudelocque's calipers, which may lead to gross error.

The amount, in the well-formed female, of the measurements instituted by Naegele for the purpose of ascertaining the presence of this deformity upon the living subject, have been given in a former section of this article. The results of the measurements of eight female pelves obliquely deformed, in five of which the ankylosed joint was that of the left side, gave the following *differences* in measurement between the two sides.

* Tafel xi. Das Schräg Verengte Becken.
† Num. 10., tafel iii. Op. cit.
‡ Heidelberg Klin. Annal., vol. x. p. 468.
§ Med. Gazette, vol. xxxii. p. 537.

	Extremes of difference between the two sides.
1. From the sciatic tuberosity of one side to the posterior superior iliac spine of the other	from 1 to 2 inches.
2. From the anterior superior iliac spine of one side to the posterior superior of the other	from 10 lines to 1 in. 11 lin.
3. From the spine of the last lumbar vertebra to the anterior superior iliac spine	from 8 lines to 1 in. 4 lines.
4. From the trochanter major of one side to the posterior superior iliac spine of the other	from 1 in. to 1 in. 7 lines.
5. From the lower border of the pubic symphysis to the posterior superior iliac spine	from 7 lines to 1 inch.

In these measurements it is to be remarked, that the *first* presents the most marked differences on the two sides. This results from the fact that the sciatic tuberosity of the ankylosed side is placed more posteriorly than the opposite one, while the posterior superior iliac spine is lower on the side free from ankylosis. Hence it results that *the ankylosis is always found on that side of which the sciatic tuberosity is nearer to the opposite posterior superior iliac spine.* These two points on a lean subject are easily to be distinguished. On the fat subject, there is, in the position of the iliac spine, a depression caused by the firmer attachment of the integuments to the bone at that place.

Another test of the presence of the oblique deformity practised by Naegele was, to place the patient upright with the back against an even wall, so that the shoulders and nates should equally touch it, and then dropping two plumb-lines, one from the spine of the first sacral or last lumbar vertebra, and the other from the centre of the lower border of the pubic symphysis. In the well-formed pelvis, the plane in which these two lines fall, forms two right angles with the plane of the wall, but in the pelvis obliquely deformed, it is an obtuse angle on the ankylosed side, and an acute angle on the side opposite; the difference between these two angles marking the degree of distortion.

Cause of the obliquely deformed pelvis. — Dr. Naegele was inclined to the opinion that the cause of this peculiar condition of the pelvis was, an *arrest of development* of one side of the sacrum and the corresponding innominate bone; with ossification of the joint instead of its normal development. The following reasons led him to this conclusion. The intimate and complete fusion of the bones into one piece; and the absence of any mark or cicatrix indicating a former separation, except a scarcely perceptible line on the upper aspect of the place of junction; a section of the ankylosis exhibiting an uniform areolar texture in the internal structure. The defective development, *in its whole length*, of the ankylosed side and lateral mass of the sacrum, as well as of the innominate bone in breadth, as particularly exhibited in the narrowing of the sciatic notch; and the analogy herein drawn, from the defective development and fusion of other bones, especially those of the cranium. The great resemblance between the several pelves affected by this disease, which argues identity of cause; original deficiency of development being more likely to produce similarity of results than the accidental and subsequent inflammation. And lastly, the presence of the distortion from the earliest period, together with the youth of the individuals affected, and the total absence of any symptoms whatever, indicating an external cause for the distortion, in the whole course of their history.

In two of the cases of this deformity, there had been present disease of the hip joint, which in one had led to the formation of a false acetabulum; but this was not, in the opinion of the above-named author, the cause of the oblique distortion. He had never seen the distortion coincident with rickets, though he suggests the possibility of such a complication.

Rokitansky also considers this deformity to be a congenital malformation, and not a consequence of fœtal intra-uterine disease.

Dr. Knox adopts the theory that the arrest of development having taken place while the ossification of the sacrum was incomplete, the whole of that side of the pelvis remains thereafter stationary in its fœtal or brute transitional form, while the other advances to complete development; and thus one side is perfect, while the opposite is simply that of an undeveloped pelvis magnified. This anatomist also states, that in the museum of Dr. Outrepont there is a female pelvis presenting the oblique deformity on *both* sides, producing a superior opening of a very elongated shape, with its broadest part towards the sacrum.

The lateral epiphysial sacral pieces, which form the auricular surface, appear in the oblique deformity to have failed in establishing a separate identity, though the presence of the sacral holes and transverse lines and grooves lead to the supposition that the number of the primary ossific points has been normal. Under this supposition, the coalescence of the sacrum and ilium would, probably, take place between the sixth and ninth months of intra-uterine life, (at which time the *characteristic* ossific points of the three first sacral vertebræ begin to appear,) by the prolongation into them of the ossifying process from the ilium or "pleurapophysis," already considerably advanced in its bony development.

Another hypothesis as to the cause of the ankylosis, is found in the occurrence of inflammatory disorganisation, after the complete formation of the sacro-iliac joint, and, as a consequence, oblique deformity of the bones. Dr. Rigby inclines to this theory, and thinks that ulcerative absorption must have existed in the joint, though probably in early life.

Since we know that the fœtus in utero is subject to similar pathological changes to those of childhood, it seems probable that a modification of the two theories may be the true statement of the origin of this formation —viz., an occurrence of inflammation and the pathological changes usually consequent upon this process in joints—such as ankylosis, happening at a period of immaturity, coincident with, or consequent upon, an arrest of development in the structures implicated, and probably having the same ultimate cause. The three cases before quoted from Naegele, in which the deficiency of the sacrum and the oblique deformity existed, but without the ankylosis, and on the other hand, the many cases in which we have ankylosis on one or both sides without the oblique deformity, show that the two conditions may occur separately and independently of each other. These cases also prove beyond a doubt, that the sacro-iliac ankylosis of itself does not produce the deformity; and, moreover, that it is not absolutely an essential, although a frequent accompaniment of this peculiar formation.

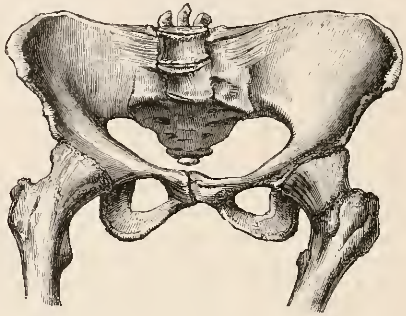
A third supposition alluded to by Naegele, that the ankylosis and oblique distortion is caused by increased pressure from the lateral divergence of the vertebral curve in early youth, seems to be contravened by the fact, that such a pressure does not produce such a result in the many instances of other pelvic deformities. The tendency to an unsymmetrical one-sided distortion in the instances before alluded to, presents many differences to, and more variations of form than, the deformity under consideration.

The *mechanism* of this deformity in respect to the line of gravity of the body falling nearer to the acetabulum of the ankylosed side, and so throwing the weight of the body more on to the corresponding leg than on its fellow, will present some similarities to that of the one-sided pelvis just mentioned; with this exception, that the bones of the obliquely ovate pelvis are healthy and not softened, and that the lateral pelvic arch is, consequently, flattened only, and not indented, the principal yielding and inward bend appearing to take place at the abnormal sacro-iliac junction, and thus the antero-posterior diameter—*i. e.* from the sacral promontory to the pubic symphysis—is increased and not diminished.

Another form of unsymmetrical pelvis is described by Rokitansky, arising from a *coalescence* of the base of the *sacrum* with the body and transverse process of the *last lumbar vertebra, on one side the median line only*, and the participation of the latter in the formation of the sacro-iliac joint on that side. The innominate bone thus obtains a higher degree of elevation, and a greater inclination to the spine, and describes a larger and shallower curve of the "linea innominata" than its fellow. The conjugate diameter is rendered greater, and there is a larger capacity on the abnormal side of the pelvic cavity. There is but slight projection of the sacral promontory, and the lumbar vertebræ are rotated, and their curve inclines to the *opposite* or smaller side, and may thus produce a lateral compensating curve in the thoracic region. In this latter particular, also, this form of pelvic distortion differs from that described by Naegele, in which the lumbar curve is towards the *abnormal* side.

I have met with two pelves presenting this abnormality. In one, that of a *female*, which is in the collection of Dr. A. Farre (*fig.* 124.)

Fig. 124.



Oblique pelvis from sacro-lumbar coalescence.

the *left* half of the sacral base is ankylosed to the corresponding side of the body and transverse process of the last lumbar vertebra, which are flattened and enlarged so as to assume the form of the first sacral, leaving a hole for the transmission of the last lumbar nerve. The lumbar transverse process of the opposite side is bifurcated, the lower division being attached by ligament to the venter ilii; and the corresponding half of the sacro-lumbar fibro cartilage remains unossified. The last lumbar spine and laminæ are connected with the sacrum by very thin plates of bone, but preserve their own distinct outline. There is *no* ankylosis of the sacro-iliac or lumbo-iliac joints. The true sacral promontory projects little, but a prominent false one is formed by the last lumbar vertebra. The sacrum is short and small, but presents four distinct sacral holes, and five pieces. The lower part of the sacrum presents an abrupt forward curve, so as to leave, with the shortness of the whole bone, little room for a fœtal head, which would, probably, require craniotomy in such a pelvis. There is a slight lumbar curve to the right or opposite side to the lumbar abnormality. The pubic symphysis, also, is removed about $\frac{1}{2}$ or $\frac{3}{4}$ of an inch to the *right* of the median line.

The other pelvis is that of a *male*, in the Museum of King's College. In this pelvis, there is complete ankylosis of both the proper sacro-iliac joints, preserving behind pretty much the outline of the sacro-iliac ligaments; and partial ankylosis of the abnormal lumbo-iliac junction, which is also on the left side. The true sacrum is large and well formed, and the posterior crest is connected with the last lumbar spine by a thin plate of bone. There is, apparently, no lateral spinal curve in this specimen.

Whether these pelves and those mentioned by Rokitansky are not similar to those described by Naegele as arrest of development of one side of the first sacral bone, is a question which can only be decided by absolute comparison of the specimens.

A greater or more advanced development of one side of the pelvis than the other is said by Knox, in a memoir "On the Statistics of Hernia," to be frequently seen, and to produce a greater predisposition to hernia on that side. The author considers it as the result of a similar want of balance between the development of the lateral halves of the pelvis to that seen, in a greater degree, in the "*pelvis obliquè ovata*," and which is also often seen between that of the true and false pelvis.

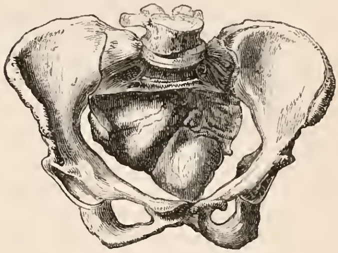
Pelvis obstructed by exostosis.—Exostoses projecting from the pelvic bones most usually proceed from their internal surfaces, in which position they are also of more serious importance in producing obstruction to parturition in the female. According to Ramsbotham, it is a rare condition of the pelvis, he having never seen an instance. Exostoses are most frequently found at the back part of the pelvic cavity, growing from the sacrum, near the sacro-iliac joint, or, according to Lever, at the last sacral piece. They are, however, by no means confined to these positions.

Many instances of this disease have been recorded, in which the diagnosis has not been verified by post-mortem examination; and it is doubtful whether many of them were not projections of the sacral promontory and lumbar vertebræ, as in a case described by Nagel in the *Frankfurter Zeitung* (April, 1778). It has been observed in the male as well as in the female pelvis.

One of the most remarkable cases of *exostosis* of the *sacrum*, producing obstruction to parturition, occurred to Dr. Haber, and is recorded in Naegele's *Inaugural Dissertation*, published at Heidelberg in 1830. The disease was said to have followed a fall while the woman was carrying a load on her head, and which was followed by pains in the back and pelvis. On afterwards becoming pregnant, the whole of the pelvic cavity was found to be filled by a bony tumour growing from the upper part of the sacrum. The Cæsarian section was performed; and the patient died soon afterwards. The tumour was found to be 7 inches long by 6 in. broad, reaching as high as the junction of the 3rd and 4th lumbar vertebræ and as low as from about 2½ lines from the apex of the sacrum. Between it and the posterior surface of the pubes there was a space of 8 or 10 lines in one part, but only a line and a half in another, the mass thus filling up nearly the whole of the pelvic brim. A section of the tumour showed large cells in the interior, communicating freely with the sacral areolæ.

Another remarkable case is recorded in the Edin. Med. and Surg. Journal (April, 1831), for which hysterotomy was performed by Dr. M'Kibbin, Surgeon to the Lying-in Hospital, Belfast. The patient had suffered a fall on the back when about six or eight years of age, which was followed by pains in the sacral region for a short time afterwards. The exostosis was of a conical form, with the base at the sacrum (see *fig.* 125.), and occupying its whole breadth at about the four lower sacral pieces, its apex projecting towards the pubis, and leaving a space of only 1⅛ inch between it and the lower part of the pubic

Fig. 125.



Exostosis of the sacrum.

symphysis. The greatest space was left opposite the superior ramus of the right pubis, where the distance of the tumour from the pubic wall was from 1¼ to 1⅝ inches, but diminished posteriorly. The patient died soon after the operation; nor was the child saved.

A less formidable case came under Dr. Murphy's observation. The tumour was about the size of an orange, and was connected to the sacrum about its middle. It was quite immoveable, and of bony hardness. The patient being in labour, craniotomy was performed; and the case did well. Another case is recorded by Van Doevern, of an osseous tumour, of the size of half a hen's egg, growing from the upper piece of the sacrum, and causing the death of both mother and child.

Dr. Kyle, of Cologne, met with a case of a woman who had borne seven children with great ease; but at the eighth labour the fœtal head became impacted by a hard immoveable tumour, as big as a hen's egg, springing from the upper part of the right *sacro-iliac joint*, being apparently the result of a pelvic abscess after the last delivery, which had, three years before, opened in the groin.

Dr. Lever has seen but one case of pelvic exostosis. It occurred in an unmarried female lunatic, and grew from the posterior surface of the *pubis*, producing retention of urine.* Lassus describes processes of bone, of a styloid shape, projecting from the posterior surface of the pubis towards the bladder.† These resulted, apparently, from ossification of the anterior ligaments of that viscus. Besides these, an exostosis is mentioned by Velpeau (*Tocologie*), protruding from the posterior surface of the right pubis, and of the size of a hen's egg a little flattened; and others by Pinæus, Ruleau, and Portal, from an ankylosed symphysis pubis.

One is alluded to by Naegele, which was as

* Guy's Hospital Reports. No. 14, April, 1842.

† Pathologie Chirurgicale (Paris, 1805, chap. 80.).

large as a filbert, projecting from the *ischium* into the pelvic cavity; and others in the same situation by Dr. Campbell and Otto of Breslau, in which indentation of the fœtal head was produced. Other cases are found in Siebold's *Journal* and Gardien's *Traité*.

Dr. A. Farre informs me that an osseous exudation from the anterior surface of the sacrum, consequent upon disease of that bone, had recently occurred in his practice, and compelled him to have recourse to craniotomy to accomplish delivery. Osseous projections at or near the sacro-iliac joints are also mentioned by Rokitansky, and are to be met with in most museums of pathology. In a large female pelvis, in the King's College museum, is a small exostosis or spinous projection at the angle of the left sacro-iliac joint, in such a position as would produce an impediment to labour in a smaller pelvis. In the Hunterian Museum are two more specimens of this kind, both on the sacro-iliac joint, one in a male, and the other in a female pelvis. Many such exostoses are seen in the subjects brought to the anatomical rooms. They seem to have the same origin as the rheumatic bony projections which are so frequently met with, in old people, in the neighbourhood of the joints, but especially in those of the spine, hip, and shoulder. Rheumatic and gouty patients seem to be predisposed to exostosis.

The *influence* of such exostoses upon parturition approaches closely to that of deformed pelvis, in the contraction of the diameters and the danger or impossibility of their removal.

The difficulty of distinguishing them, when of considerable size, from pelvic deformities, is sometimes very great. Their hardness is not so characteristic as to mark them from the projections of the sacral promontory; their shape, compared with external measurements and the history and appearance of the patient are the chief means of diagnosis.

Osteo-sarcomatous tumours sometimes produce pelvic obstruction, and generally grow from the joints or ligaments. One case occurred to Grimmell of Kisbaden, and is recorded in a letter to Naegele (Dec. 1835). Cæsarian section was performed in consequence of a tumour of this kind, weighing $1\frac{1}{2}$ lb., attached to the periosteum only of the right sciatic spinous process and wall of the corresponding acetabulum. It had followed a fall, which had been succeeded by pains in the sacrum, a sense of weight in the right thigh, and ischuria. Stark performed hysterotomy successfully for a tumour attached to the lower sacral vertebræ and innominate bone. It was immoveable, but *soft* in various parts, as well as could be detected "*per vaginam*."

This characteristic will distinguish these tumours, in diagnosis, from exostosis; their partial hardness, from fibrous tumours; their immobility, from tumours of the soft parts; and their attachments to the side of the pelvis, from the fœtal head.

Obstructions from fibrous tumours attached to the pelvic ligaments. These are of rare occurrence, and have been found chiefly connected with the sacro-sciatic ligaments.

The most remarkable examples are those related by Dr. Drew in the *Edin. Med. and Surg. Journal* for 1805 (vol. i. p. 20). The first of these tumours was taken from the body of a woman, who had died in consequence of its pressure upon the pelvic viscera. It was 16 inches in circumference, of a hard, gristly texture, with no appearance of vascularity, and was attached by a strong root, of the same texture, to the left sacro-sciatic ligaments, and interposed between the bones and viscera, but with no other attachment to the surrounding parts. The second tumour was excised by Dr. Drew, by a formidable operation, from the pelvis of a woman in labour, who was afterwards safely delivered and recovered perfectly well and very speedily. The tumour was 14 inches in circumference, and weighed 2 lbs. 8 ounces. It grew from the right side, and filled the whole cavity of the pelvis so completely as to admit of one finger only being passed between it and the pubis, considerably interfering with the neck of the bladder and urethra. It was separated easily from the circumjacent tissues.

A somewhat similar case is related by Dr. Burns; but, in this instance, the attachments of the tumour were much more extensive; reaching from the pubic symphysis to the sacrum, and adhering intimately to the pelvic brim, being attached also to the obturator internus muscle, urethra, vagina and rectum, and apparently developed in the recto-vesical fascia. It was hard, somewhat irregular, and scarcely moveable. The patient being in labour, Dr. Burns, by a bold operation, in which but little blood was lost, removed the tumour, which required to be almost dissected out. The woman was soon after safely delivered of a still-born child, and, after some peritoneal inflammation, recovered.

Fibrous tumours attached to the pelvic parietes are distinguished from the fœtal head and tumours of the soft parts, by the immobility of their attachments; from exostoses, by their want of bony hardness; and from osteo-sarcomatous tumours, by their uniformity of structure to the sense of touch.

Carcinomatous growths commonly affect the bones of the pelvis, by advancing from the contained viscera, the uterus, rectum or ovaries. Dr. A. Farre mentioned to me a case in which the innominate bones were so much infiltrated by cancerous matter, from a tumour commencing in the uterus, that they could, with great ease, be cut with the knife, presenting a condition very similar to the bones affected with *mollities ossium*.

Pathology of the Pelvic Joints. — The pelvic joints, like all other joints in the body, but much less frequently than many, are subject to inflammation and its consequences in such structures—viz., ulceration, suppuration, and ankylosis. They are also, probably more frequently, subject to original malformation, coalescence, and anomalous constructions of a congenital origin.

Ankylosis is the most frequently seen in the sacro-coccygeal joint. It is also met with in the sacro-iliac, and sometimes, but most rarely, in the pubic symphysis. Ankylosis of the *coccyx* is one cause of pelvic obstruction and protracted labour, and as such has been before adverted to. Meckel describes ankylosis of the coccyx to be more frequent in males than in females, particularly in such as have long-continued equestrian habits.

Coalescence of the bones composing the *sacro-lumbar* articulations have been before described as producing deformed pelvis. This formation almost universally results from an original aberration of development, and not from ankylosis as a subsequent pathological result. Sometimes it occurs on both sides with hypertrophy and transformation of the last lumbar transverse process. In many of the instances recorded of six sacral pieces, and in the pelvis drawn after Murphy (see *fig.* 113.), a complete coalescence of this kind probably existed.

Ossification of the *sacro-iliac* joint has also been referred to in connection with the "*pelvis obliquè ovata.*" It is, however, by no means confined to pelves presenting that deformity.

In the Museum of King's College is a well-formed male pelvis, with ankylosis of the sacro-iliac joint on the left side, the bones presenting no other traces of disease or deformity.

In the experience of Rokitansky, it is rare that the bony union in ankylosis of the pelvic joints extends through the whole of the opposed articulating surfaces, but generally takes place by bridge-like processes, passing from one margin of the joint surface to the opposing margin, so as to enclose the fibro-cartilage in a kind of bony capsule. It is not ascertained whether the fibro-cartilage itself ossifies, or, as he thinks is most likely, becomes absorbed before the ossifying process from the adjacent bones. This author does not mention whether this process takes place without previous inflammation, or follows the analogy of other joints, in which pain, inflammation and absorption of the cartilages, usually precede the ankylosis. The instances of incomplete ossific union mentioned by him to be most common have most probably a *rheumatic* origin, like the smaller exostoses previously referred to, and arise from ossific deposits in the circumferential ligaments, without the interior structures being affected. Meckel describes ossification of the sacro-iliac joints as those most frequently seen, and that it most commonly occurs on the *right* side, and is to be accounted for by the greater pressure borne upon the right leg! He considers, also, that ossifications of this joint usually take place without preceding inflammation, from a gradual change in their substance and in the fibrous tissues around them.

In a specimen of ankylosed *pubic symphysis* described by J. P. Mitchell, and given by Hull in his 2nd Letter, the whole of the fibro-cartilaginous disc was converted into a smooth equable bony substance. A few other cases of complete ankylosis of this symphysis are recorded by Wagner. In a case described and figured by Sandifort*, the pubes were united on their posterior and upper surfaces by an osseous bridge in the position of the ligaments, leaving a chink between the bones in front. In the same pelvis the right *obturator membrane* was also extensively ossified, as well as a considerable portion of the right capsular ligament of the hip joint,—all these circumstances indicating a rheumatic origin. Ossification of the *ligamentum arcuatum* is also mentioned as sometimes interfering with the urethra. Cases of imperfect ankylosis of the pubic joint are also mentioned by Siebold, Voigtel, Walter, and Bonnard.† All writers agree that ankylosis of this joint is rare. Dr. W. Hunter had never seen an instance of it.

Ossification of the *sacro-sciatic ligaments* is mentioned by Meckel as sometimes existing, and even more commonly than that of the pubic symphysis. Such a condition, if present in the female during parturition, would offer great obstruction to the passage of the head through the inferior strait, from its unyielding nature, and resistance to the extension of the coccyx. It is, however, not sufficiently common to be enumerated as one of the ordinary obstacles to parturition.

A different result of inflammatory change in the pelvic joints, is that which gives rise to the *separation* of the bones at their articular surfaces. This, as a pathological process, takes place most frequently by deposits of pus, as a consequence of puerpal fever, which may entirely destroy the joint, and separate the bones. From its more exposed position and more open structure, this change has been most frequently observed in the symphysis pubis. A case of this kind is described by Dr. W. Hunter, and many others have been observed.

A more remarkable separation of the pelvic joints is to be ascribed to a *congenital* origin. It is one in which the pubic bones and with them, in a minor degree, the sacro-iliac auricular surfaces, are separated, more or less widely, and held together by a ligamentous band. Instances in which this occurs to the extent of a third of an inch, are mentioned by Professor Otto, as being pretty frequent.‡

Probably one of the most extreme cases of this kind is seen in a preparation at present in the Hunterian Museum. It is the pelvis of a woman, which was presented, as I am informed, by Mr. Mayo, of Winchester, and taken from a case which died in the infirmary of that town. The pubes are separated to the great distance of 4¾ inches; and connected by a ligamentous band of about the width, in its present dried state, of from ½ to ¾ of an inch. The pubes are more elevated than normal, with their articular extremities turned outward, and the symphy-

* Observ. Anat. Path., b. i. p. 115., tab. 8.

† Journal de Med. de Paris, 1778. t. xxxix. p.433.

‡ Compend. of Human and Comp. Anatomy.

sial surfaces forwards, by the action of the adductors and obturator externus. The lateral curvature of the sacrum is considerably flattened out, and also the cotylo-sacral rib of the ilium. The sacro-iliac joints are each opened in front, for the space of about half an inch, stretching the anterior ligaments. The great space between the pubes is evidently obtained by the flattening of the linea innominata, as well as by the shortening of the innominate bones, in breadth, and their abnormal vertical or wall-sided position. The resulting *diameters* are; — antero-posterior, from the sacral promontory to the inter-pubic ligament, 4 inches; the inter-cotyloid, $6\frac{1}{2}$ inches; and between the sciatic tuberosities, $6\frac{1}{8}$ inches. This condition, according to Meckel, is rarely met with without an analogous congenital fissure in the bladder and walls of the abdomen. Walter, however, mentions one case.*

Other *congenital abnormalities* of the pelvic bones are mentioned by Otto and Rokitansky. In the *siren* formation, the coccyx and lower extremities are entirely wanting, and the lateral parts of the pelvic bones are fused together, the outlet of the pelvis being nearly completely closed, and the parts presenting the appearance of the pelvis as we have seen it in the Cetaceans and Fishes. Their development seems to have been arrested at that period of fœtal life in which this condition is normally, though transitorily, present. In some monstrosities, the sacrum also is wanting, or one or both the innominate bones, with the correspondig lower extremities; or these parts may be stunted or coalesced.

Influence of hip-joint disease upon the pelvis. — Caries and necrosis of the pelvic bones, although sometimes resulting idiopathically, or from bedsores and abscesses in the muscular sheaths or lymphatics, yet chiefly occur as the consequences of *coxalgia*, and have a tubercular origin. The formation of false acetabula and the other pathological results of this disease or accidental malposition belong more especially to the pathology of the Hip-joint.

A preparation of one of these in the Hunterian Museum may be, however, appropriately described in this place, inasmuch as it would produce, if occurring in a parturient female, an obstruction to the fœtal head, analogous to an exostosis. The head of the femur has become displaced into the obturator foramen, and about it an osseous deposit has taken place, apparently in the obturator membrane, which forms a smooth dome-like projection into the pelvic cavity, corresponding in size to the head of the femur. The subject is a male one, and the carious and light condition of the bones and the irregular ossific projections, indicate the results of disease.

An interesting change in the position of the pelvic bones after hip-joint disease, is described by Rokitansky.†

* Von der Spaltung der Schambeine. Berlin, 1782.

† Pathological Anatomy, p. 259. Sydenham Society's translation.

The dislocation of the femur upwards, which is commonly the result of coxalgia, is followed by a wasting of the innominate bones, especially of the ilium. They assume a more vertical direction, and, at the same time, their inclination to the spine, as well as the lumbar curve, is considerably increased.

If this condition be present on both sides, there is general enlargement of the pelvic cavity, due partly—to a general attenuation of the bones, causing the disappearance of the projections at the pectineal eminences, the sacro-iliac joints and the cotyloid walls, and partly to a flattening out of the *linea innominata*. The ischia become dragged outwards and separated, the pelvic cavity shallower, and the sub-pubic angle more obtuse.

The last result is attributed by Hülshof to the dragging of the rotator muscles, from the displaced femur on the sciatic tuberosities, upon which the support of the trunk mainly falls in this condition of the joint. In the pelvis of a woman mentioned by Dr. Hull, however, in whom both the femurs had been dislocated backwards, the transverse diameter of the brim was diminished to $4\frac{1}{2}$ inches, and the antero-posterior diameter of the outlet was diminished to only 2 inches, from the tilting forward of the lower part of the sacrum, or rather probably, from the turning of the lower part of the innominate bones backward by the displaced femurs, acting on the axis of the sacro-iliac joints.

If the disease be one-sided only, as is most commonly the case, and the diseased joint be much used, the *tuber ischii* of that side becomes everted, the innominate bone bent outwards, the distance from the pubic symphysis to the anterior superior iliac spine lessened, and that side of the pelvic cavity enlarged. The pelvic cavity is, on the other hand, contracted on the sound side, towards which also the spinal curvature inclines, from the principal support of the body falling on that side. When ankylosis has taken place, the innominate bone is bent outward at the acetabulum, in the osseous cicatrix; the ilium is placed more inwards and forwards, and the ischium inwards and backwards; and while the pubic symphysis is drawn towards the diseased side, the sacral promontory is turned to the healthy side of the pelvis. In some instances, the pelvic inclination is less, instead of greater, on the diseased side, which is also raised higher than the other. This variation is attributed by Guerin to the action of the psoas and iliacus muscles, which sometimes in these cases impress a deep furrow upon the iliac wings, over the edge of which they play. There is no doubt, that the posture to which the patient may have been most accustomed, has a great effect in producing such differences, as already explained in the foregoing pages.

Fractures and Dislocations *of the pelvic bones.*—The *sacrum*, according to Boyer, is less frequently found fractured than the other pelvic bones, because of its thickness, strength, spongy texture, and deep-seated position. When fractures of this bone do happen, they are most commonly found at the lower part, which is less protected by the above peculiarities. They occur chiefly from direct and great violence, which generally injures also other parts of the pelvis extensively, seriously affecting the nerves of the sacral plexus, so as to produce paraplegia and retention of urine, as well as extensive injury to the soft parts, such as result in effusion of blood, peritonitis, and sloughing of the integuments. Fractures at the lower part are much more easy to diagnose than those of the upper, which are seldom discovered till after death. In the former case, the lower fragment is generally drawn forwards by the action of the great glutei and coccygei muscles, so as to press upon and interfere with the functions of the rectum, through which it may be felt by the finger. It will also produce great pain on moving the legs, which may lead to its discovery, when more serious injury is not present.

The *coccyx* when normally placed is rarely fractured, on account of its great mobility and small size. It always happens by direct violence. When ankylosed, it is more frequently broken, and instances of this have been before mentioned, in relation to the obstruction of the outlet in parturition which it occasions. It is diagnosed by the mobility and grating of the fragments, and by the pain caused by the action of the great glutei muscles. *Dislocation* of the coccyx is said to have occurred backward in difficult labours, and to have been followed by abscess, but these cases have been most probably fractures like those just mentioned.

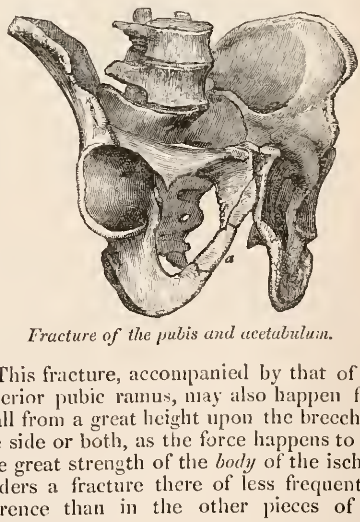
Fractures of the *innominate bone* generally occur on one side only, where the greatest part of the force has fallen, but sometimes on both. They are most frequently found in the ilium—which is most exposed, but often implicate both the ischium and pubes. They may be confined to one part of the bone ; in which case they are found chiefly about the iliac crest and wing. Boyer relates a case in which the inferior anterior iliac spine was broken off by the kick of a horse. Cases are not unfrequently seen where the anterior superior iliac spine and a portion of the crest are broken off. Sometimes they are comminuted in, and radiate from, the cotyloid cavity, such fractures generally resulting from direct violence against the lateral pelvic arch, and acting on the head of the femur so as to drive it inwards through the pelvic wall.

Fractures of the pelvis, like those of the spinal column, are seldom present without *dislocation* also of the sacro-iliac or pubic joints. This results from the circular arrangement of its bones, and from the laws of its mechanism, explained in the first section of this article. Thus, when force is applied so as to compress the pelvic circle from before backward (as commonly the cause of these fractures is such compression by the wheels of a loaded cart or other vehicle), then the cotylo-sacral arch yields inwards at its haunches,—the sacro-iliac joints, the anterior ligaments of which are torn, and the articular surfaces separated in front. At the same time the pubic tie yields either at the symphysis or in the superior rami.

The innominate bone may be entirely dislocated upward or backward, generally on one side only. A case is related by Cloquet, in which this was the case on both sides, the pubic symphysis, at the same time, separated ½ an inch, the pubis and ischio-pubic ramus were broken, and the bladder ruptured. Another case, where the left innominate bone was displaced upwards, was treated successfully by Chaussier.

The ligaments and fibro-cartilage of the symphysis pubis are usually torn, the latter generally carrying with it a portion of one of the bones ; or the superior ramus is broken at its weakest part, above the obturator foramen, or it separates from the other innominate pieces. In most cases the ischio-pubic ramus of the same side also yields at or near the point of suture, which is its thinnest and weakest part, and the obturator foramen is again penetrated. This results from the operation of the force upon the unsupported ischio-sacral arch and its tie, after the other has yielded. A preparation exhibiting such a fracture is found in the King's College Museum. In this case the superior pubic ramus has separated in the acetabulum from the other pieces of the innominatum in the line of the Y-shaped suture, while the fracture through the ischio-pubic ramus extends upwards, along the side, and into the centre of the pubic symphysis (*fig.* 126.).

Fig. 126.



Fracture of the pubis and acetabulum.

This fracture, accompanied by that of the superior pubic ramus, may also happen from a fall from a great height upon the breech, on one side or both, as the force happens to fall. The great strength of the *body* of the ischium renders a fracture there of less frequent occurrence than in the other pieces of the innominatum.

Fractures of the innominate bones seldom occur without *displacement*, produced usually—not by subsequent muscular action, which is kept in check by their balance of power, and by the extensive ligamentous and fascial attachments and the opposing fractured surfaces,—but by the original direct violence.

By such displacement of comminuted and spicular fragments in the true pelvis, the bladder and urethra, particularly if the former be distended at the time of the accident, often suffer great laceration, which may even extend to the peritoneal investments and open the cavity of the abdomen. Such extensive injuries are invariably followed by extravasation of the urine into the pelvic areolar structures or peritoneal sac; and violent peritonitis carries off the patient, even if he survive the first shock of such a formidable accident. The external soft parts, also, generally suffer greatly from the violence, and from the great extravasation of blood which usually takes place from the torn vessels. Gangrene may, in these cases, succeed to a great extent, and destroy the patient. It is these injuries, and their consequences to the soft parts and internal structures, that render fracture of the pelvis, like those of the cranium, so dangerous and fatal to life.

The *diagnosis* is drawn from the pain and difficulty of moving the lower extremities, and from the mobility and crepitus of the fragments, felt on placing the hand on the iliac crest, the pubic spine, and sciatic tuberosity consecutively and moving the leg. The crepitus is most distinctly felt by the hand which rests on the pelvic bones, and scarcely at all by that which moves the leg. This useful comparison will distinguish these fractures from those of the neck of the femur. If one ilium be dislocated upward and backwards on the sacrum, and at the same time separated from the other bones by a fractured acetabulum, the femur is drawn up with the ilium, the trochanter turned forwards, the knee and foot turned inwards, and the whole limb shortened, so as to resemble a dislocation at the hip-joint. Deeply-seated fractures, however, often pass undetected, from the rigid contraction of the muscles, the great pain experienced on motion, and fear of injuring the viscera more extensively. They will be more easy to detect on the thin subject, and on the female.

In one of the cases figured and related by Sir Astley Cooper in his Surgical Essays (plate 2. fig. 6.), the head of the femur had been driven by violence, applied laterally, through into the pelvic cavity, carrying a comminuted portion of the acetabulum with it. The fracture was Y-shaped, and had radiated from the centre of the acetabulum pretty nearly in the line of the suture,—as we have before remarked in fractures here and in the ischio-pubic ramus. A fracture near or in the latter suture also existed. The limb presented the appearance of a dislocation of the femur backwards. In another case, the posterior part of the acetabulum was broken off, the fracture passing across to the pubes, both innominate bones being broken and displaced, and the femur dislocated. The pubic symphysis was separated about an inch, the fibro-cartilage adhering to one bone only. The knee and foot were turned inwards, and the whole limb shortened two inches; but it was more moveable than in a dislocation, and crepitus was felt on cautious extension being made. In a female whose pelvis had been crushed by a cart against a wall, a fracture was found passing through the body of the left pubis and the left ascending ischial ramus. Both the sacro-iliac joints had separated, part of the osseous sacral auricular surface of the right joint having come off with the ligaments. The pubes were separated at the symphysis. Motion and crepitus were felt on applying one hand to the ilium and the other to the pubis, and the posterior superior iliac spine projected upwards considerably. Through the vagina, the pubes were felt projecting into the vaginal cavity. There was much blood effused into the pelvis, and the patient died, sixteen days after, from sloughing of the soft parts.

Otto mentions that, in the Museum of the Veterinary College at Copenhagen, are specimens of horses' pelves, fractured by excessive muscular action.

Sir A. Cooper mentions three cases of fractured innominate bone which had recovered. Two were fractures of the ilium, easily detected by the mobility of the crista and crepitus. The third was a fracture of the ischio-pubic ramus about the suture.

Rokitansky found that fractures of the pelvis rarely united without displacement. One of Mr. Barlow's successful cases of Cæsarian operation was necessitated by the results of a fracture of the left innominate bone, which produced an elevation of the head of the thigh bone, shortening of the limb, and lameness. The contraction of the pelvic diameters resulted mainly from a projection backwards at the symphysis pubis, which was supposed to be caused by ossification of the disarticulated joint, and which reached to within half-an-inch of the sacrum. Burns states that he has seen extensive pointed ossifications projecting nearly 2 inches into the pelvis, in consequence of fractured acetabulum. Naegele also mentions cases in which a bulging of the acetabulum inwards caused obstruction to parturition. Dr. Lever has also seen a bony process, more than an inch long, encroaching upon the pelvic cavity, in a male subject, after fractured acetabulum. Sometimes, after fractures of the pubis, the formation of callus has considerably interfered with the functions of the urethra. When ankylosis takes place at the sacro-iliac joint, after dislocation of the ilium backwards, the pelvis assumes a shape closely resembling the *pelvis obliquè ovata* of Naegele. A preparation of this kind is mentioned by Dr. Ramsbotham, as existing in the Museum of University College.

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(*John Wood.*)

REPRODUCTION, VEGETABLE. (VEGETABLE OVUM.) Before the microscope was placed in the hands of the vegetable physiologist, the conditions by which he was surrounded in the investigation of the processes by which the embryo is formed, differed widely from those which exist at present. From the absence of means of observation, the phenomena of reproduction could only be studied in the Phanerogamia. Even as regards the highest cryptogamous plants, very little had been ascertained; while the Algæ and Fungi were involved in the most complete obscurity. But in the Phanerogamia it was already known that two kinds of organs were essential to the production of the embryo, and something had also been learnt of the mode of their combination. No sooner were these facts established, than, with a readiness of which innumerable examples present themselves in the history of physiological investigations, they were at once seized upon to serve as the ground of a comparison between the animal and vegetable kingdoms; and naturalists soon passed to the conclusion that the organs in question were of distinct sexes, or, in other words, stood in the same relation to each other as those of animals. The analogy seemed sufficient for the mind to rest upon; and the doctrine derived from it was received as indisputable.

The influence exercised by the state of things we have just described, may be traced in two directions:—In the first place, a strong tendency is even now observable in the minds of naturalists, especially in this country, to approach the subject from the same point of departure as before, when the circumstances were so different. The appearance of greater simplicity among the higher plants, was entirely dependent on conditions belonging exclusively to the observer; that is to say, on the imperfection of the means of observation. Now that so many of these imperfections are removed, to take the Phanerogamia as our starting point in approaching either this or any other general question in vegetable physiology, is evidently unreasonable; we must commence our investigation where there are fewest complications—namely, at the unicellular plants. From this point we must ascend from class to class, following as closely as may be the natural order of complexity of organisation.

A second result of the same causes is the confusion which so frequently arises in the employment of terms which are derived from the animal kingdom, such as "male," "female," "ovum," &c. As our knowledge of the subject becomes more accurate, the grounds upon which the assumed correspondence between the reproductive organs of plants and animals rests appear less substantial. The only analogies, indeed, which can possess any real value are those occurring between the lowest members of the two series. This is the only point at which the two kingdoms are in mutual contact, and consequently it is here only that an actual correspondence can be traced through successive consecutive modifications.

The subject of the following article is the origin and development of the *germ*, or, in other words, the reproduction of plants by means of germs.

Considering it as a conclusion, respecting which there can remain very little doubt in the present state of vegetable physiology, that every existing plant must have originated as a single cell, there are two modes in which this may be supposed to have taken place. In the one case, a cell originally forming a part of the tissue of the parent, and not previously distinguished in any respect from its neighbours, suddenly assumes a new activity which it did not before possess. To this change the term "Verjüngung," or, as it is rendered by Mr. Henfrey, "rejuvenescence," has been applied, and is most expressive of its nature. A cell in which there has previously been a gradual diminution in the intensity of vital manifestations, recovers the capability of development which it possessed when first formed. Now, however, the formative force by virtue of which the whole subjects the development of all its parts to its own, being abated and weakened by age, the rejuvenescent cell becomes individualised and is transformed into the rudiment of a new plant, in accordance with a capability of development, which resides entirely in itself. This process is called gemmation.

In the other case, the cell from which the new plant originates, manifests from the first moment of its existence conformity to law, on the one hand, in its anatomical relations to the organs of the parent upon which it is supported, or within which it is enclosed, on the other, in the mode in which its development commences — its transformation being the result of an activity inherent in it, not as an individual cell, but as being a part of the parent, and still under the control of its formative force. It is to this cell that the name germ is alone applicable in the restricted sense in which it is generally used; namely, as expressing not only that it will, if it live long enough, transform itself into an embryo, but that it presents itself uniformly in the same species under the same anatomical conditions.

The term "vegetable ovum," placed at the head of this article, is employed in order to connect it with the preceding one on the "animal ovum," to which it is intended to form a sequel. In its usual acceptation in vegetable physiology, the word means the generative product of the Phanerogamia only. And even if we were to extend its meaning so far as to include all those varieties of germ, for the development of which two organs mutually dependent on each other for the accomplishment of their reproductive functions are necessary, we should still be obliged to disregard one half of the vegetable kingdom.

Part I.

Algæ, Fungi, and Lichens.

1. *Reproduction by means of Zoospores.*— Among the most simply organised infusory animals are included several genera, which are admitted by all naturalists to present, in the aggregate of their characters, as many points of resemblance with plants as with animals. They agree with plants in their chemical constitution, in the mode in which they react on the atmosphere, and in their green colour. The Euglena viridis, which is so common in all our shady ponds, though in active motion during the greater part of its life, manifests at other periods a condition of plant-like repose. The contractility displayed in its rapid and ever-varying changes of form is a property which, there can be little doubt, manifests itself frequently among undoubted plants;* so that the transition from the Euglenas to many of the forms of the Protococcus-like Algæ is almost insensible. The elaborate researches of Cohn on the so-called Protococcus pluvialis, have unfolded many facts of the greatest importance in relation to this subject. The well-known permanent form of this plant is that of a globular cell, furnished with a distinct colourless membrane, and containing in its interior a semifluid protoplasma, in which numerous green or red granules are embedded. Cohn found that when water is added to Protococci in this condition, they immediately become the subjects of an active reproductive process. In the interior of each cell are formed, by the division of its contents, secondary cell-like bodies, the number of which is always either two, or a power of two. These bodies, which possess no distinct membrane, either give rise to stationary cells similar to their parent, or, as is by far more frequently the case, especially when the number of newly produced individuals is large, they become pear-shaped, fusiform, or oval; at the same time they are endowed with the power of

Fig. 127.

Cell of Protococcus pluvialis, containing moving Zoospores, about 25 diam. (Cohn.)

active motion, and are furnished with a pair of vibratile cilia, emanating from their anterior

Fig. 128.

Free Zoospores of the same. (Cohn.)

extremities. In the course of their further development, these actively moving bodies, which we shall call Zoospores, become invested with a distinct membrane. This seems to be a preparatory step to the cessation of their movements; for shortly afterwards they are observed to lose their vibratile cilia, and assume a form which corresponds more or less completely to that of the mother cell. In many cases, however, before this result is accomplished, a second reproductive process commences in the still ciliated zoospore. A division of its protoplasmic contents, similar to the first, takes place, and a second generation of zoospores is set free, each of which is capable, after exhibiting active motion for a longer or shorter period, of becoming a spherical, motionless cell, in all respects similar to the original parent. Thus an individual Protococcus in its stationary form, may reproduce itself either directly, or with the intervention of a second generation. In the former case, the germ may either become at once an individual similar to its parent, or may pass through a preparatory period, during which it is not only provided with motor organs, but manifests in the protoplasm of which it is formed, a property of contractility resembling that of animals. Facts similar to the above are described by Braun as occurring in another unicellular Alga (Ascidium acuminatum). This species, which is found attached to stones or other objects, resembles the Protococcus pluvialis in its general form. By the division of the protoplasma which lines its cell-wall, numerous zoospores take their origin. These are pear-shaped, and at the apex of each is observed a pair of vibratile cilia.

2. In the above-described plants we have examples of the occurrence of zoosporous reproduction under the most simple condi-

* The presence of contractility of the substance in true plants is still doubted by some physiologists. One of the most accessible proofs of its existence is to be found in the motions of the tapering growing extremities of some species of Oscillatoria. Here we have changes of form of the substance of the plant, rapidly succeeding each other, and developed independently of the action of any external stimulus. These motions may be observed with perfect facility and occur under the most simple conditions.

tions. In the history of their development we have an epitome of that of all the more simple Algæ. In the family of Protococci the type may be said to be included to which all the green and olive-coloured Algæ, with the exception, on the one hand, of the Desmideæ and their allies, on the other of the Fucaceæ, may be referred. Among the Desmideæ, indeed, is placed one genus, that of Pediastrum, in which the zoosporous is the only form of reproduction which has been observed. Pediastrum consists of a disc of cells, which are usually eight in number, and contain a protoplasma, which possesses a generally diffused green colour. The first step in the reproductive process consists in the separation of the protoplasma into a green and a colourless portion. The former, after collecting into a central mass, becomes divided into numerous secondary masses, the number of which is always a power of two. From the latter is formed a transparent gelatine-like investment which lines the parent cell. After the completion of these changes the original cell-wall is ruptured, and the whole contents escape in a mass. No sooner has this taken place than the corpuscles into which the green protoplasma has divided, commence an active motion in the interior of the gelatinous cell in which they are included, and in fact display in every respect the form and peculiarities of zoospores. They are not, however, as in every other example with which we are acquainted, destined to display their activity beyond the narrow limits within which they originate. In a short time their motions become languid, and finally cease, while they arrange themselves in a beautifully regular geometrical order which corresponds exactly to that of the cells that constitute the adult Pediastrum. The next change observed is the disappearance of the gelatinous membrane, and the investment of each of the zoospores with a distinct covering of its own. From this there results a disc-like body, which, in a short time, assumes all the characteristics of the original parent.*

3. Taking these simplest of unicellular plants as our point of departure, we pass to the consideration of the confervoid Algæ, many of which, though they are but little elevated above the Protococci as regards their structural elements, present a general appearance which at first sight recalls that of plants very much higher in the scale of organisation. Thus in Bryopsis and its allies, in which the tubular frond branches in the most complicated manner, the whole consists essentially but of a single cell, the cavity of which is continuous throughout. When the formation of zoospores is about to take place, all that is observed in a Bryopsis is the accumulation of the green granular protoplasma towards the extremities of the tubular branches. In these situations the cavity of the tube becomes completely filled, while at some point in the neighbourhood of each accumulation, the tube membrane becomes sacculated so as to present a nipple-shaped projection. In the meantime the accumulated protoplasma is observed to have given rise, by its division, to numerous green bodies, the forms of which cannot yet be distinguished, owing to the closeness with which they are packed together. No sooner, however, is this process complete, than a remarkable phenomenon, corresponding to that already described in Protococcus, manifests itself. The crowded zoospores, now completely developed, at once commence their characteristic motions. From this results an appearance of confused agitation, to which the term "swarming" has been applied by the Germans. A minute aperture, or pore, is

Fig 129.

a, termination of tubular frond of Bryopsis crowded with zoospores; *b*, the same, after the escape of its contents. Each of these exhibits the lateral pore; *c*, fully formed zoospores in active motion. *a* and *b* 150 diam, *c* 200 diam.

then found at the extremity of the nipple-like projection, apparently in consequence of the absorption of the cell-membrane at its apex. The zoospores now begin to escape, at first one by one, afterwards more rapidly, until at last a few only are left occupying the cavity of the tube.*

4. In the simplest forms of jointed confervoids, the frond consists of a series of cells superposed one upon the other, each of which is capable of producing zoospores independently of the rest. In the vegetative state, each contains only a green protoplasma. The reproductive process is the same in every respect as in the Bryopsideæ, the opening by which the zoospores make their exit, being situated at the upper part of the cell, immediately below the septum, which divides it from its successor. In other cases (as in Microspora), the zoospores escape by a kind of

* The development of Pediastrum has been described by Braun (Die Verjüngung in der Natur) as well as by Caspary (Botanische Zeitung, 1850, S. 786.). The description in the text is after Braun, with whom Caspary agrees in every important particular.

* Thuret, Recherches sur les Zoospores des Algues. Ann. des Sc. Nat. xiv. 217.

dislocation of the tube, each cell dividing into two in a plane parallel to the septa.*

5. The Ulvaceæ, among which the frond has no longer the form of a filament, but assumes that of a membranous expansion of juxtaposed cells, still present the same phenomena to our notice. In the cells set apart for the formation of zoospores, the green protoplasma is increased in quantity, at the same time that it becomes accumulated towards one point of the cell-wall. As the zoospores are formed, they are observed to converge with their apices towards this point. The phenomena attending their escape from the parent cell are similar to those which we have already noticed.

6. In some genera, which seem to be closely related in form and structure to the Bryopsideæ, we observe this important difference, that the zoospores are developed in an organ specially destined to this purpose, which presents peculiarities of form distinguishing it from every other part of the branching tubular frond. Thus in the genus Derbesia distinct spore cases are to be observed, the cavity of which does not communicate with that of the frond. These organs, which are of an oval form, take their origin in the same manner as the ordinary vegetative branches of which they are modifications. A young branch which is destined to become a spore case, instead of elongating indefinitely, begins, after having arrived at a certain length, to swell out into an ovoid vesicle, in the cavity of which a rapid accumulation of protoplasma takes place. The next change which occurs is the separation of this protoplasma from that of the rest of the plant with which it was before continuous, so as to give rise to an oval and opaque mass, which soon becomes surrounded by a distinct membrane. As the result of the division of this mass, a number of pyriform zoospores, each of which is furnished with a crown of cilia, are set free. Many other genera have been described by Derbes and Solier†, in which the relations of the spore cases to the frond are similar to those which exist in Derbesia, although the forms presented by the organs in question are infinitely various.

7. The researches of the authors above alluded to, along with those of M. Thuret, have shown us that in many families of the olive-coloured Algæ, the occurrence of zoosporous reproduction is no less general. The zoospores, however, although they resemble in their general form those of the plants which we have been considering, differ from them not only in respect of their olive colour, but in the arrangement of their cilia. These organs, which are always two in number, are

Fig. 130.

Sporangium of Ectocarpus siliquosus, 240 *diam.*

Ectocarpus is one of the simplest forms of olive-coloured Algæ, consisting of branching, conferva-like filaments. The extremity of any of the branches is capable of being converted into a sporangium by the absorption of the septa of the terminal cells. The zoospores are arranged in regular horizontal layers, the positions of which are indicated in the empty sporangium by faint markings of its membrane.

usually of unequal length, and emanate not from the beak, but from the reddish-coloured point in its neighbourhood. The longest is directed forwards, being closely applied to the colourless beak; while the other, which seems during the motions of the spore to serve as a rudder, assumes an opposite direction. In many genera a peculiarity exists, the signification of which is not yet completely understood—that, namely, of a double fructification. The ovoidal sporangia (*oosporangia*, Thur.), which have been frequently described as single spores, in reality contain numerous zoospores. The other form (*tricho-sporangium*, Thur.) consists of a series of small cells joined together so as to form a narrow and generally short filament. Each of the cells contains a zoospore, which, according to the observations of Thuret, is no less capable of germinating than the one produced by the oosporangium. In the genus Cutleria there is observed, for the first time, another feature of great interest and importance; namely, the appearance of two kinds of organs which seem to be opposed to each other as regards their reproductive functions. The sporangia (trichosporangia) of Cutleria, not only differ from those of other genera, in respect of their greater size, but

* In the genus Œdogonium, the protoplasma of each joint, instead of being converted into a number of zoospores, goes to form but one, which differs from those of other genera, in the first place in being considerably larger, and secondly, in presenting around its rostrum not two, but a number of cilia, which are arranged in the form of a crown. (See Thuret, *l. c.* p. 226.)

† Derbes and Solier, Sur les Organes reproducteurs des Algues. Ann. des Sc. Nat. xiv. 260.

present well-marked distinctive peculiarities of structure. The frond consists of olive-coloured, irregularly divided *flabelli*, on each

Fig. 131.

a, a portion of one of the tufts, or sori, of Cutleria, showing the mode of attachment of the filaments which support the sporangia to the surface of the frond; *s*, a ripe sporangium. Two others, half ripe, are also seen. Each is divided into eight compartments, in each of which is formed a zoospore,—200 diam.; *b*, zoospores; *c*, the same in various stages of germination; the earliest stage to the right, 300 diam.

side of which, tufts (*sori*), consisting of the reproductive organs, intermixed with hair-like bodies, are scattered at irregular intervals. The sporangia, and so-called antheridia, are borne by different individuals, but their positions and arrangements on the frond are identical. The former consist of oblong or club-shaped bodies, which are supported by hyaline pedicles, set into their inferior extremities. The cavity of each sporangium is divided by three transverse partitions into four cavities, each of which is again bisected by a longitudinal median septum. In each of

Fig. 132.

Portion of one of the sori of the male plant of the same.

The ripe sausage-shaped vesicles, which contain antherozoids, are shaded. Others are shown which have already discharged their contents, 180 diam. The transverse markings, much too distinct in the engraving, indicate a tendency to the formation of compartments similar to those which present themselves in the sporangia.

the resulting cavities, zoospores are to be found, which, though they altogether resemble in structure those of the other olive-coloured Algæ, are about three times as large. The supposed antheridia of Cutleria communicate to the tufts of which they form a part, their characteristic orange colour. The organs themselves are elongated, sausage-shaped vesicles: they contain a greyish, granular matter, in which, as the organ becomes ripe, indications may be observed of a division into several concentric layers; the more internal of these layers being distinguished from those next the surface by the greater intensity of the orange colour which they present. After

Fig. 133.

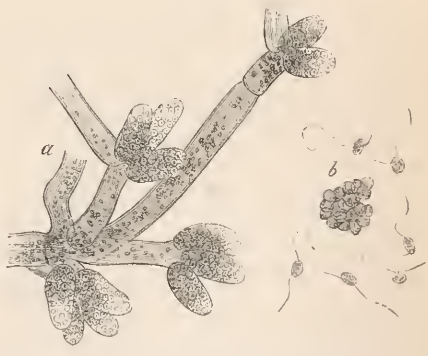
Contents of antheridium of the same, 400 diam.

Each antherozoid is an oval hyaline corpuscle, which moves in the direction of its long axis. It exhibits towards its posterior extremity a coloured granule, from which springs a pair of cilia of unequal length. The longer of the two, which oscillates rapidly, is directed forwards; the shorter, which is motionless, backwards.

the discharge of the contents of the antheridium, it may be observed to consist of a transparent vesicle, which, like the analogous female organ, is divided by transverse and longitudinal septa into eight communicating cavities.

8. With the organs last described we think we need have little hesitation in comparing the structures to which the same name has been applied, as they occur in the Fucaceæ. The fructification of these plants is, as is well

Fig. 134.



a, antheridia from the conceptacle of Halidrys siliquosa, with the filaments on which they are supported, 200 diam.; *b*, antherozoids, 400 diam.

known, enclosed in spherical cavities, situate under the epidermis of the frond, which are called conceptacles, and may be male, female, or hermaphrodite, according to the organs which they contain. The male conceptacles present in their interior an arrangement of branched filaments, or hair-like organs, which, taking their origin from the surrounding cellular tissue, converge towards the pore. At the summits of these filaments, the so-called antheridia are supported, which consist of little ovoid transparent vesicles. They contain, in their early condition, a granular protoplasmic material, but as they approach maturity, the so-called antherozoids make their appearance. These last are hyaline corpuscles, not exceeding about $\frac{1}{5000}$ of an inch in their longest dimension. Each contains a granule of a greyish or reddish orange colour, from which the organs of locomotion emanate. The form of the zoids differs according to the genus. In Fucus, they are bottle-shaped, and each possesses a pair of cilia, one of which, the shortest, is directed forwards from the neck, while the longest emanates from the coloured point and is pointed backwards. In Halidrys, the zoid is ovoid or spherical, and the longest cilium is directed forwards. In Fucus and several other genera, the transparent vesicle in which the zoids are immediately contained, is itself enclosed in a second of similar form. At the period of maturity this last gives way at its apex: the internal sack is expelled, and at once finds its way towards the external opening. In the meantime its delicate membrane disappears, and the liberated zoids commence their active motions.

9. Although the antherozoids of the Fucoideæ differ from the zoospores of the other olive-coloured Algæ, in their not possessing the power of germination, there are yet remarkable points of correspondence between them, in their form, structure, and mode of development. Both are composed of a hyaline protoplasma, and the position of the coloured granule, as well as the arrangement of the cilia, corresponds. They differ, in the first place, in size, and secondly, in respect of the chlorophylle granules, which are present in the zoospore, but absent in the antherozoid. As regards the question of their functional signification, they may be considered, on the one hand, as the elements of a male secretion, and the organs in which they are contained, as antheridia; on the other, we may look upon them as the formal representatives of structures destined in other families to the performance of functions of which they are themselves incapable. In favour of the first of these views we have no direct evidence, and must trust entirely to analogy. We know that in Cutleria and its allies, the zoospores display the power of germinating without the slightest reference to the presence or absence of the secretion of the supposed male organ. Further, if, as all observations which have been hitherto made, tend to prove, the zoospores of all the green Algæ, and of so many of the olive-coloured, normally germinate under the condition of the constant non-existence of such organs, it is difficult to see why an exception should be made in favour of those of other families in which they are present. As regards the Fucoideæ, we have certainly no evidence whatever that the antheridia perform any function, either more or less important in the reproductive process.

10. In the family of Vaucheriaceæ, the zoosporous reproduction is remarkably modified by the substitution of a single multiple zoospore, of large size, for a number of smaller ones. The frond of Vaucheria consists of a branched tube, and much resembles in general form, that of the Bryopsideæ, from which the Vaucheriæ in their vegetative condition differ only in respect of the arrangement of the chlorophylle. The commencement of the formation of zoospores is announced by the condensation of the green protoplasma in the rounded terminations of the branches of the plant. This condensation is accompanied with an enlargement of the cylindrical filament, which soon appears club-shaped, and is completely occupied by a confused and opaque dark-green mass. Shortly afterwards a septum is formed, which limits the terminal portion of the tube. Within the separate cavity thus formed, the mass of protoplasma becomes further condensed; its margin being surrounded by a clear space which intervenes between its external surface and the tube membrane. This body, which possesses an oval form, is the future zoospore. No sooner is it completely developed than the membrane which encloses it gives way at the apex, and it begins to insinuate itself through the resulting narrow opening. Having completely freed itself, it forthwith commences an active progressive motion, which is accompanied by a circumvolution round its axis. The zoospore at this period possesses no distinct or consistent investing membrane, as is evident from the fact, that if, during its escape, it divides accidentally into two — a circumstance which not unfrequently happens, from the relative narrowness of the opening through which it has to pass — each part is complete in itself and capable of germination. Its whole surface is covered with vibratile cilia, which are apparently connected with an epithelium-like structure. In this arrangement there seems to be an indication of a tendency to a division into smaller particles, by the melting together of a number of which the whole may be conceived to be formed. Like all zoospores its period of active motion is short; it soon becomes stationary and begins to germinate.* The zoospores of Vaucheria seem to correspond closely with the motionless spores of the true Dictyotaceæ (Dictyota, Padina, &c.), as well as with those of the Fucaceæ. In the case of the latter, the accuracy with which their structure and germination have been studied, has enabled us to follow out the analogy more closely. In speaking of the an-

* See Thuret, Ann. des Sc. Nat. 2^e S. xix. 269; Vaucher, Hist. des Conferves d'Eau douce, p. 246; Karsten, Die Fortpflanzung der Conferva fontinalis, Bot. Zeit. 5 Stück, 1852.

theridia (§ 8.), we described the general form of the conceptacles. In the monœcious and diœcious Fuci, the female conceptacles are distinguished from the male by their olive colour. The spores are developed each in the interior of a perispore, which is borne on a pedicle emanating from the inner wall of the conceptacle. They make their escape by the rupture of the perispore at its apex. At the moment at which this takes place, the spore is perfectly simple, except that in one or two species the surface is covered with cilia, which seem to resemble those of Vaucheria. Soon afterwards, a remarkable series of changes occurs, consisting in the splitting of the endochrome into a number of masses — usually eight — each of which becomes isolated, and finally assumes the form of a smooth and spheroidal sporule, provided with an investing membrane. About twenty-four hours after the completion of this process, germination commences. It consists in the budding out of the membrane of each sporule, at some point of its surface, into a nipple-shaped projection, which in the following forty-eight hours, elongates into a cylindrical tube; shortly afterwards the whole body of the sporule is converted by repeated division into a mass of cells, in which condition it has been by many writers mistaken for the original spore, and described as such. The Vaucheriæ present the peculiarity of a double mode of reproduction. In the earlier periods of the growth of the plant, there occurs the successive formation of aggregate zoospores of large size at the termination of the branches, as above described. In the older fronds these are no longer observed, their place being taken by organs producing germs which are capable of retaining for a long period their power of development.

11. In that most remarkable plant the Saprolegnia ferox, which is structurally so closely related to Vaucheria, though separated from it by the absence of green colouring matter, we find a corresponding analogy in the history of the development. Its vegetative life is, in fact, divisible into two well-marked periods, each characterised by a special mode of germformation. During the first, the only one with which we have at present to do, swarms of zoospores which rapidly succeed each other, are formed at the closed terminations of the cylindrical filaments. The mode of their origin, agrees with that of the aggregate zoospore of Vaucheria. The protoplasma accumulates in the swollen extremity of the filament, and a septum is formed in exactly the same manner as in that plant; while the mass of protoplasma is now observed to be limited by a distinct surface. At this point the resemblance ceases; the protoplasmic membrane divides, just as in the spore-cases of the zoosporous Algæ, into particles, which, as the period of maturity is approached, become more and more easily distinguishable from each other. These particles are the future zoospores. Soon they detach themselves from their connection with the membrane which encloses them, and with each other, and present the globular or ovoidal form characteristic of their perfect condition. In the meantime the external tube membrane buds out at its apex, so as to form a conical projection; as the zoospores become ripe, a gentle oscillatory motion is seen in the upper part of the spore-case. This is accompanied with a compression of its contents, in consequence of which its membrane gives way at its weakest point,— viz. the apex of the terminal conical projection. In its most perfect condition, the zoospore of *Saprolegnia* consists of a pyriform, protoplasmic, membraneless corpuscle, which is furnished with a pair of *cilia*, emanating from its apex. It is remarkable for the short duration of its motion, the cessation of which is immediately followed by germination.*

Fig. 135.

Sporangium of Saprolegnia ferox, during the expulsion of the zoospores, 200 *diam.*

(All the figures, from 129 to 135 inclusive, are from Thuret.)

* For the history of the second period of the vegetative life of Saprolegnia, see below, § 19. It is only under the most favourable conditions that the zoospores of Saprolegnia assume the form described in the text. Very frequently at the period of their escape, they are spheroidal corpuscles unendowed with the power of motion, if not incapable of germination. In this case, according to Anton de Bary, the completion of their development takes place outside of the spore-case. He describes the accumulation of the escaped, but imperfectly formed, zoospores in rounded heaps (*Köpfchen*), which remain for several hours in contact with the terminations of the tubes from which they have escaped, and finally become invested with a cellulose-membrane. Within this membrane their development is completed; and when they at last escape, they

12. In the process of the formation of zoospores in Saprolegnia, we have an intermediate step between that of the zoosporous Algæ on the one hand, and that of a class of plants which is usually placed among the Fungi on the other. I allude to the Fungi included in the class Cystosporeæ of Leveillé; on the intimate structure of this, as well as of many other allied groups, there are as yet but few researches. We have, however, enough in the beautiful monograph of Cohn, on Pilobolus, to enable us to discover that it is structurally more closely allied to the Algæ than to the Fungi. We shall take Pilobolus as an illustrative example.

13. Pilobolus has an ephemeral existence. The spore germinates about mid-day; the plant grows till evening, ripens during the night. In the morning the spore-case bursts, and the whole disappears, leaving scarcely a trace of its former existence.

In correspondence with the future mode of life of the plant, the spore-cell displays in its germination, a tendency to development in two opposite directions, by the formation of two sacculations, the first, cylindrical — the root; the second, ellipsoidal — the stem. Shortly afterwards the young plant is seen to consist of two cells, of which the inferior is elongated and branched at its lower extremity—root-cell; while the superior is ellipsoid, and acuminated above. The former contains a quantity of protoplasma, which lines, as a distinct layer, the internal surface of its wall. The first change which is observed consists in the accumulation of this protoplasma towards the apex of the cell, at which point the membrane buds out, so as to form a bead-like head. Within the cavity of this organ — the future spore-case, further accumulation takes place, until it is entirely filled with a coloured granular material; while the rest of the cell, from which it is as yet undivided, contains only a clear fluid. The process is completed by the formation of a septum just as in Vaucheria, which takes place early in the morning. This is immediately followed by the "cleaving" of the protoplasma, and its division into numerous small cells, which are the future spores. As the plant reaches the termination of its existence, the cell on which the spore-case is supported, enlarges at its upper part from the increase of its fluid contents; the septum is pushed upwards, and presses on the contents of the spore-case. At last in the course of the forenoon, the tension of the wall of the spore-case becomes so great that it gives way at its junction with the supporting cell with such force, that it is thrown like a miniature bomb for several inches.*

14. The Fungi which agree in their development with the species above described, are limited in number, and belong for the most part to the genera Pilobolus and Ascophora (Mucor). The formation of the spore differs entirely from the process of strangulation, which Schleiden considers as characteristic of the Fungi. On the other hand, the analogies between Pilobolus and Vaucheria are of the closest kind; even the ephemeral periods observed in the development and ripening of the reproductive apparatus, being the same. The root-cell of Pilobolus the inferior of the three of which the whole plant is composed, is as permanent as the tubular frond of a Conferva. From it emanate tubular, unjointed root-like processes, from the upper surface of which spring out at intervals young spore-cases, in every respect similar to the first-formed plant. These creeping rootlets constitute the vegetative system of the plant, which, like that of the Fungi, is perennial.

15. *Reproduction by conjugation.*—From the number of the observations which, during the last few years, have been made on the subject of the phenomena of conjugation, no less than from the variety of the conditions under which they have presented themselves, we are bound to assign them an important place in a systematic description of the reproductive process. Decaisne included in his group Synsporeæ all the Algæ in which the phenomena in question were then known to present themselves — namely, the genus Zygnema and its allies, along with Closterium, which last, for the same reason, he separated from the Desmideæ. The beautiful researches of Mr. Ralfs have taught us that all the genera of the Desmideæ conjugate in the same manner as Closterium. More recently analogous phenomena have been observed in the Vaucheriaceæ, and in that remarkable plant Saprolegnia ferox, which so closely resembles Vaucheria in every respect, except its green colour. We shall describe in succession each of the examples which have been mentioned.

16. Among the Desmideæ, conjugation has been more frequently observed and described, and was known to take place at an earlier period in Closterium, than in any other genus. The earliest description is that of Morren, which is to be found in the Bulletins of the Academy of Brussels, for 1836, and is among the most accurate that we possess. The crescent-shaped cell forming the frond of Closterium is, as in the Desmideæ, composed of two similar halves, to the plane of junction of which its long axis is perpendicular. It differs from other genera in the absence of a median constriction, the junction being only indicated by a faint line in the external mem-

are pear-shaped, and possessed of cilia. These observations I have been altogether unable to confirm, and am inclined to believe that the escape of the zoospores in the spheroidal form is to be attributed to an arrest of development, as in all cases which I have observed, the total disappearance of the spores has supervened shortly afterwards. — Anton de Bary, Beit. z. Kentnisse der Achlya prolifera. Bot. Zeit. 28 St. 1852. For further information on Achlya, see Unger, Linnæa, 1843, p. 129.; Nägeli Zeit. f. wiss. Bot. B. i. H. 1, 2. Pringsheim, Nova Acta Ac. L. C. 1851.

* Cohn, Die Entwickelungsgeschichte des *Pilobolus crystallinus*. Nova Acta Ac. L. C. p. 496. 1851.

brane.* When two fronds are about to conjugate, they place themselves parallel and opposite to each other, with their concave surfaces facing. We next remark that the cell membrane partially gives way at the line above mentioned, the two halves of each Closterium separating slightly on the side opposite its fellow, but remaining in contact on the other side. The openings are soon observed to be occupied by cushion-like projections of the internal membrane, which squeeze out between the valves. From the fact that the cavity of the internal membrane is double, or rather that each half of the Closterium possesses an independent primordial membrane, it follows that each of the projections above mentioned consists of two distinct *sacculi*. Soon the two double cushions come in contact; they are at first perfectly colourless, but shortly afterwards become filled with green granular matter, and press so closely together as to be no longer distinguishable. It is next observed that from the junction of the four sacculi, two canals have resulted, each of which soon swells out in a hemispherical form, corresponding to

Fig. 136.

Conjugation of Closterium.

The two fronds are connected by *two* delicate tubes, each of which contains a hemispherical germ-cell closely invested by its membrane. The two germ-cells, which are in opposition by their flat surfaces, appear as one. About 40 diam.

that of a mass of green granular matter which now occupies its cavity. This mass is soon invested by a delicate membrane, which, in the progress of development, thickens and presents an uneven surface. The two bodies which thus take their origin are the germ cells. They soon become free from the structure in which they were formed, and, according to Morren, display for about fifteen minutes after their escape an active motion. After this period, the motion ceases, and they attach themselves to a foreign body. Morren has observed their germination. The spherical germ lengthens first at one, then at the opposite extremity, so as to assume the characteristic crescentic form of the plant. Its green contents divide into two masses, each of which is invested by a separate primordial membrane, and occupies one of the future segments of the frond. In a short time the young Closterium completely resembles the adult. It is worthy of remark, that in the abnormal cases in which only one germ results from the conjugation of two individuals, only one of the halves of each empties itself, the other remaining unaltered.*

In other families of Desmideæ, the process of conjugation, although variously modified as to its less important details, is essentially the same as that which occurs in Closterium.†

17. In the Zygnemaceæ, confervoid plants, which seem to have a close relation with the Desmideæ, the phenomena of conjugation have been long known. The frond consists of a series of cylindrical cells, which lengthens indefinitely by repeated division of its elements. Here, as in the Desmideæ, it is the last-produced cells in the filament which take part in the process of conjugation. In Spirogyra the union of two cells belonging to opposite filaments takes place by the expansion of one side of each, so as to form a papilla, or short tube with a rounded end. The ends of the two projections then come into contact, become slightly flattened as they are pressed against each other, and unite. The double wall formed by their union, dissolves, or is broken through, so that a free passage is established between the two cell cavities. Upon this, the whole of the chlorophylle previously arranged round the inside of each of the cells, becomes a confused mass, which soon forms itself either in the cavity of one of them, or in the connecting canal, into a globular or oval smooth spore, invested with a colourless cellulose membrane. Having arrived at this condition, it remains several months — from the autumn of one year to the spring of the following,—without undergoing any change of form.‡ During this period two new membranes are produced within the first by the secretion of cellulose on the surface of the primordial utricle. Of these two, the external is of considerable thickness, and of a yellow colour. The internal, which may be considered as the proper membrane of the spore, is delicate and

* Morren, Ann. des Sc. Nat. 1re Ser. p. 325.

* According to Morren, the process above described is not the only one by which the reproduction of Closterium takes place. In the green granular matter contained in a frond, there occur spherical corpuscles which, according to that observer, are capable of reproducing the parent plant. He has described and figured their germination, and it is worthy of remark that his figures of the earliest stages of Closteria thus developed, correspond closely with those of the earliest stages of the plant as observed by Mr. Ralfs, who, however, assigns to them a different origin. (See *British Desmideæ*, tab. xxvii. m.)

† It is clear that if the formation of germs by conjugation were the only provision for the reproduction of the species, in the Closteria and many other families of Desmideæ, its total disappearance must result, inasmuch as the conjugation and consequent destruction of a pair of Closteria can only give rise to an equal or less number of new individuals. But the other mode of reproduction already alluded to as occurring in Closterium, and which has been so well described by Mr. Ralfs in the other Desmideæ, affords an effectual safeguard against their otherwise possible extinction.

‡ Braun has observed the germination of the spores in a specimen of Spyrogyra setiformis which had been collected for eleven months. (Braun, *l. c.* p. 144.)

transparent. Germination consists in the growing out of this membrane at one end of the spore into a many-celled filament, which escapes through a lacerated opening in the external membranes, and gradually assumes the character, and appearance of the parent plant. At the same time a tubular elongation of the same membrane of limited growth is formed in the opposite direction, which is the rudiment of a root.*

18. In a species of Palmelleæ (Palmoglea macrococca) in which the whole individual consists of a single ovoid cell containing green granular matter, and usually multiplying itself by successive division, the phenomena of conjugation present themselves in a somewhat different and very remarkable form. Here two cells, probably the result of a series of divisions, undergo a complete union, affecting not only their contents, but also their membranes. They coalesce as completely at their points of contact, as two contiguous drops of water, the result of their union being a cell which differs in no respect from its predecessors, except in the greater thickness of its walls, and in the complete conversion of the chlorophylle of its contents into oily globules. Like the spore of the *Zygnemaceæ*, it is destined to a long period of inactivity, after which, by the successive division of its contents, it gives rise to a new series of individuals, similar to those that preceded it.

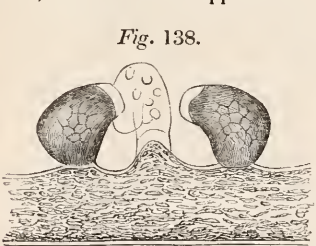
19. We have still to consider the most remarkable condition under which conjugation takes place among the Algæ. The evolution of the aggregate zoospore of Vaucheria has been already described. In the plant which results from its germination, Karsten has observed that along the course of those filaments which come in contact with the atmosphere are formed organs of a peculiar structure. They originate like the ordinary branches, as nipple-shaped buddings out of the cell-wall, which are distributed in pairs along the whole course of the older filaments. In every pair of organs, one elongates so as to form a closed

Fig. 137.

A portion of the tubular frond of Conferva fontinalis, showing the arrangement of the sexual reproductive organs. About 30 *diam.* (Karsten.)

tube, which curves round into a spiral form, like the leaves of a Pilularia, while its fellow soon ceases to grow in length, but swells out into a globular or oval form, about three times as wide as the other. At first both contain chlorophylle, which, in the tubular organ, is soon replaced by colourless globules. In the meantime its fellow, which resembles a dark-green-coloured globe, supported on a short pedicle, alters in form, its cell-wall extending into a nipple-shaped projection on the side next the tubular organ, with which it finally comes in contact. This condition lasts for some time, but it does not appear determined

Fig. 138.



A single group more highly magnified, about 200 *diam.*

Two of the egg-shaped organs which contain the germs are represented; one of which is in contact, by its smaller end, with the tubular organ which occupies the centre. (Karsten.)

with sufficient distinctness by Karsten's observations, that an actual interchange of the contents takes place. All that we learn as certain is, that after the completion of what he calls the act of fructification, a newly formed cell appears in the cavity of the globular organ, which shortly after separates from the mother plant. In this instance, as in those above described, conjugation is preceded by the conversion of the green granular contents of the conjugating cells into oil globules. The germ thus produced retains its power of development for several months, and gives rise to a new plant resembling its parent in structure.*

20. In Saprolegnia, which is morphologically so closely related to Vaucheria, and like it, in its earliest state of existence, produces zoospores, we obtain, by the germination of these zoospores, plants which produce reproductive organs of an entirely different character. These, when completely formed, consist of spheroidal cells, each supported on a cylindrical pedicle. Each contains in its interior a number of round spores (from five

* Vaucher, Conferves d'Eau douce, p. 46; Pringsheim, Annals of Nat. Hist. June, 1853. (Trans. by Mr. Henfrey.)

* Karsten, Die Fortpflanzung der *Conferva fontinalis*. (Bot. Zeit. 1852, 6 Stück.)

The process of which the details have been so well described in the above memoir, was known to Vaucher, and is mentioned by him in his "Histoire des Conferves d'Eau douce" (p. 17.). See also Nægeli (Vergl. Algensyst. p. 175.); Hassall (British Freshwater Algæ. vol. i. p. 175.); and Thuret (Annales des Sc. Nat. 2nd Ser. 1843), who gives a figure illustrative of the conjugation of *Vaucheria hamata*. In *V. polysperma*, a species described and figured by Hassall (*l. c.* Pl. iv. f. 6.), the spore-bearing organs are very much more numerous than the curved tubular organs, a fact for the explanation of which observations are as yet wanting.

or six to forty), which differ from the zoospores, not only in their external form, but in possessing a distinct investing membrane. This complication of structure corresponds with the capability of retaining their vitality for a long period. They may be found in an unaltered condition in the water in which the parent plant has grown for many months after the total destruction of the latter; and it is to them, doubtless, that we must attribute the extraordinary facility with which the Saprolegnia makes its appearance whenever the peculiar conditions it requires present themselves.* On the filaments which produce the above-described spore-cases, there are developed among them, and at the same time with them, slender, worm-like branchlets. These, as they reach the spore-cases, attach themselves firmly to them, and even sometimes wind round them in a regular manner. An actual interchange of contents, however, has not yet been observed.†

21. *Reproductive organs of the red Algæ or Florideæ.*—In this group of plants we unfortunately know too little of the origin and development of the germ-producing organs, to compare them with the forms which prevail in other groups. It is altogether beyond the limits of the present article to describe in detail all the perplexing varieties of structures to be found in the Florideæ which may be supposed to have some relation with the reproductive function. It will be sufficient to mention the three leading forms that are met with, and which may at all times be easily identified, in spite of the innumerable subordinate modifications that they undergo. The first form, to which the term *polyspore* is usually applied, is that of a gelatinous or membranous pericarp or conceptacle, in which an indefinite number of sporidia are contained. This organ may be placed either at the summit or in the axil of a branch, or it may be concealed in or below the cortical layer of the stem. In other cases a number of sporidium-bearing filaments emanate from a kind of placenta at the base of a spheroidal, cellular *perisporangium*, by the rupture of which the sporidia which are formed from the endochromes of the filaments, make their escape. Other forms, which it does not seem necessary to mention, are observed: they all agree in one particular, viz. that the sporidium is developed in the interior of a cell, the wall of which forms its perispore, and the internal protoplasmic membrane (endochrome), the sporidium itself, for the escape of which the perispore ruptures at its apex.

22. The second form is much more simple, and consists of a globular or ovoidal cell, containing in its interior a central granular mass, which, as the organ arrives at maturity, divides into four smaller quadrant-shaped spores, which finally escape by the rupture of the cell-wall. This organ is called a tetraspore; it takes its origin in the cortical layer. The tetraspores are arranged either in an isolated manner along the branches, or in numbers together, surrounded by a whorl of smaller branchlets. In some cases the form of the branches which contain tetraspores is so completely modified by their presence, that they assume the appearance of special organs, which are called *stichidia*, as, for example, in Dasya.*

23. It is with respect to the third kind of reproductive organ, the antheridium, that the greatest differences of opinion exist; all observers, however, agreeing as to the general signification to be attached to it. The antheridia are always produced on different individuals, but in precisely the same situations as the tetraspores and polyspores. They are "agglomerations of little colourless cells either united in a bunch, as in Griffithsia, or enclosed in a transparent cylinder, as in Polysiphonia, or covering a kind of expanded disc of peculiar form, as in Laurencia."† According to the researches of Derbes ‡ and Nägeli §, each of these cellules contains a spermatozoid. Nägeli describes it as a spiral fibre, which, as it escapes, lengthens itself in the form of a screw. Derbes, on the other hand, describes it as "a hyaline globule, furnished with a flagelliform appendage, by means of which it agitates itself with a very active motion, which lasts for some moments." According to M. Thuret, who certainly is to be considered a higher authority than either of the above mentioned, each cell of the antheridium is occupied by a hyaline corpuscle, spherical in Polysiphonia, ovoidal in other genera. These corpuscles, however, whose contents are granular, offer no trace of a spiral filament, but are expelled from the cells by a slow motion, which Thuret compares to that observed in the expulsion of the tetraspores from their theca. The antheridia appear in their most simple form in Calithamnion, being reduced to a mass of cells, composed of numerous little bunches, which are sessile on the bifurcations of the terminal branches. The woodcut represents the antheridium of Griffithsia, in which species, it is produced like the tetraspores, in a sort of lateral involucre of verticillate branchlets. Each of these bifurcates, and bears at the bifurcation a pyramidal antheridium, which

* Pringsheim, *l. c.* N. A. A. L. C. 1851. p. 417. All that is required to obtain a living specimen of this singular plant, is to allow the body of any small animal, such as a fly or spider, to float for a few days in rain water, exposed to the light. By this method a crop of Saprolegnia may be obtained at any season.

† Braun. *l. c.* p. 318.

* See H. H. Harvey, Nereis Boreali Americana, Part ii. *passim.* New York, 1852. The best descriptions of the organography of the Florideæ will be found in the Essay of Decaisne on the Classification of the Algæ in the Ann. des Sc. Nat. 1842; and in Nägeli's Zeitschrift, f. w. Bot. Heft. 3 & 4. Zürich, 1846.

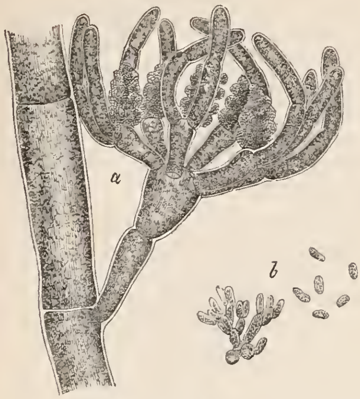
† Thuret, Ann. des Sciences Nat. 3me Ser. xvi. 14.

‡ Derbes, Ann. des Sciences Nat. 3me Ser. xiv. 261.; Thèse de Botanique, p. 25. Paris, 1848.

§ Nägeli, *l. c* H. 3 & 4. S. 224. Zwei Bemerkungen, &c. Bot. Zeit. 1850. 32 Stück.

is composed of little bunches of hyaline cells, which are arranged round a central axis,

Fig. 139.



Antheridia of Griffithsia, 30 diam.

a, a kind of involucre is formed by a whorl of six verticillate branchlets, at the points of bifurcation of each of which is borne an antheridium; *b*, terminal tuft from surface of antheridium, along with a few of the hyaline vesicles, 300 diam. (Thuret).

formed of larger cells placed end to end. At the junctions of these, smaller branches are given out, upon which the hyaline cells are sessile. These last possess a diameter of about $\frac{1}{2500}$ of an inch.

From the above details it will be seen that great difficulties lie in the way of a comparison between the reproductive organs of the Florideæ and those of other families. Nägeli considers them to present a strong analogy with those of the Hepaticæ, with which he places the Florideæ in a parallel position. We shall see, as we advance, how little ground there is for such a view.

The Florideæ are triœcious plants: the tetraspores, polyspores, and antheridia being never found together in one individual.

24. *Characeæ.* — Although we are well acquainted with the structure of the reproductive organs of the Characeæ, we are, as yet, able to perceive only subordinate relations between them and those of other plants. These organs are of two kinds; the one being destined to the production of a germ, the other to that of antherozoids. The former is an oblong oval body, which is placed at the junction of two segments of the articulate tubular stem. It consists of an oval germ-cell, invested by two envelopes. The outer of these is remarkable for the arrangement of the five tubular cells of which it is formed, which are twisted spirally round the central parts, and form by their ends, at the summit, a crown of five teeth.

The germination of Chara has been observed and described by Vaucher.* The development of the germ, which ripens in autumn, does not take place until spring. It consists in the budding out of the central cell at its apex so as to form a single tubular stalk, just as in the lower Algæ.

25. The antheridium of Chara is an orange-red, and globular body, which is attached to the stem immediately below the germ-producing organ. It consists of eight concave, rectangular valves, joined at their edges so as to form a hollow sphere. At each suture there is a partition, which is directed to the centre of the sphere; while from the centre of each valve there springs a cylindrical cell, the axis of which is perpendicular to its inner surface, so that each cell approaches the centre of the sphere by its extremity. The whole antheridium is supported by a ninth cylindrical cell, which is inserted by its base into the stem of the plant, and passing up between the corners of the four inferior valves, approaches the other eight cylindrical cells at the centre. From the extremities of the nine cells, there emanate a number of flexible tubes, which are

Fig. 140.

a, flexible tubes from antheridium of Chara. From most of the segments the antherozoids have escaped; two are in the act of escaping: *b*, fully formed antherozoids. 400 diam. (Thuret.)

divided by transverse partitions into a number of segments. In each segment or cavity an antherozoid is contained. Each antherozoid is a spirally coiled fibre endowed with a power of active motion, which is displayed as soon as it is removed from its cell. The motion is of two kinds—of progression, and of revolution round the axis. According to Thuret, two cilia emanate from each antherozoid, a little behind its anterior extremity, and it is to these organs that the motion is to be attributed.*

26. *Summary.*—If we take into consideration only those families of the Algæ in which the phenomena of reproduction have been more or less completely investigated, we shall find that all the instances of the occurrence of bodies to

* Vaucher, Mém. Soc. Hist. Nat. de Genève, tom. i.

* For further information see K. Müller, Die Entwick. der Characeen, Bot. Zeit. 1845, p. 393. Kaulfuss, Die Keimung der Characeen. Leipzig, 1825. Varley, On the Structure of Chara in the Microscropic Journal. Thuret, Ann. des Sc. Nat. xvi. p. 18.

which the term "germ" may be applied in the sense of the definition given at the outset, may be included in one of two classes. The first comprises zoospores and zoosporoid bodies; the second, all those forms of germ which require for their development a previous combination of two parts or organs, complementary to each other as regards their reproductive functions.

27. *Zoospores.*—Of zoospores we recognise two kinds, simple and aggregate. The simple zoospore is a pear-shaped or ovoidal body: it is composed of transparent, colourless homogeneous plasma, throughout the whole of which, with the exception of the smaller end (rostrum), granules of colouring matter are scattered. It possesses no investing membrane, but is provided with a pair of cilia, the directions and positions of which differ according to the class. Every zoospore possesses a single granule of a red or reddish-brown colour, which is always placed in the immediate neighbourhood of the colourless rostrum. Its characteristic *motion* is a constant progression in the direction of its axis, around which the whole zoospore at the same time revolves, the transparent rostrum being always directed forwards. As regards the *chemical composition* of the zoospore, the transparent and colourless plasma is a nitrogenous compound, coloured brown by iodine. The cilia, as far as their reactions can be ascertained, resemble the plasma from which they emanate. As to the constitution of the coloured granules which are scattered throughout the plasma, we have as yet no direct observations; but from the form which they exhibit being that which is always assumed by starch, not only among the Algæ, but also in the green Infusoria, there can be little doubt that they are composed of that principle, in mechanical combination with colouring matter and a fat.

28. In passing from the condition of motion to that of repose, or, in other words, in germinating, the zoospore is not subject to any suspension of its vegetative activity. From the moment that it is set free from the parent plant to that at which it begins to develope from itself a new plant similar to the parent, it continues to grow uninterruptedly.

29. Of the aggregate zoospore, the best-marked example is that which has been fully described in Vaucheria. In comparing the termination of a fructiferous filament of Vaucheria, with the sporangium of Saprolegnia, we can at once satisfy ourselves that these are corresponding structures: the distinctive difference being, that in the one the whole protoplasma contained in the termination of the tube is collected together to form a single large zoospore, while, in the other, it is subdivided so as to form a multitude of small ones. In other words, the single zoospore of Vaucheria takes the place of the collection of zoospores contained in one sporangium of Saprolegnia. This fact is all that we mean to imply by the use of the term aggregate.

30. *Zoosporoid bodies.*—Among these we include the antherozoids of Cutleria, of the Fucaceæ, of the Florideæ, and of the Characeæ. Of the relations of the first two to the true zoospore in form and development, we have already said enough in the preceding pages. Those of the antherozoid of Chara are not so close; and the structure of the organs in which they are developed, differs so essentially from any structure met with in any other family, that it is inexpedient to found any notions of their nature or formal relations upon such slender analogies as may exist. In the case of the Florideæ, the correspondence between the antherozoids and the zoospores of other Algæ, is still less traceable; but the peculiar arrangement of the bodies in question — their being always developed in different individuals, though in similar positions as regards the organs of vegetation— leads us irresistibly to the conclusion that they have a mutual relation, or are in some degree complementary to each other in function; and as we know the production of germs to be the function of the one, it is reasonable to assign their fecundation to the other.

Germs, whose development is dependent on the combination of two organs the reproductive functions of which are complementary each to each.—Of these it is the leading characteristic that they do not necessarily pass at once, as soon as they are set free from the parent, into active development. If the necessary conditions of temperature and moisture are absent, they are capable of remaining in a state of repose, without losing their power of germinating. This state may last for weeks, or even for months. Their second characteristic is connected with the first; viz. that they are always provided with a distinct investing membrane, on the strength of which their power of resistance to external agents may in part depend. This is well seen in the spores of the Desmideæ and Zygnemaceæ.

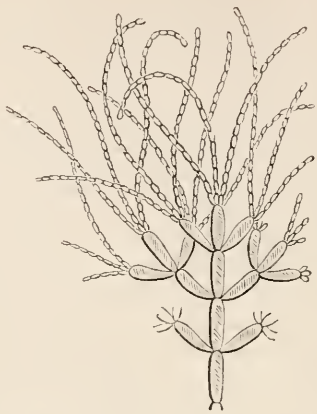
31. There remain a few examples of germ-like bodies of uncertain signification, which are included in neither of the above divisions. Such are the various forms which occur among the Florideæ, the stationary spores of Saprolegnia, and others, of which, as they are still imperfectly known, sufficient has been said in the preceding pages.

32. FUNGI AND LICHENS.—While, on the one hand, the Fungi and Lichens present an endless variety in the organs which constitute their reproductive system (receptacle), their vegetative system (*mycelium*, *stroma*, *flocci*, *hypothallus*, *&c.*), on the other, preserves a remarkable degree of uniformity. It always consists of a network of cylindrical hollow filaments, usually divided at irregular intervals, but sometimes simple. In the latter case the whole network, however complicated it may appear at first sight, is in fact only a ramified cell. This structure, which, in its simplest form is the immediate result of the germination of the spore, is the most permanent portion of the plant, inasmuch as, although every part of it, considered separately, is transitory, the vegetation of the whole is continuous, and its duration unlimited. It is from it that the organs which constitute the reproductive sys-

tem take their origin, and, as its presence is essential to the existence of the plant, it may be considered to represent, functionally, the stem of other vegetables.

33. On the formation and development of the germ in the Fungi, comparatively very few researches have yet been made which are not so deficient either in completeness or accuracy as to be useless. This being the case, the best mode of treating the subject seems to be to select those isolated facts and observations which are most to be depended upon, and arrange them in such a manner as to serve as a foundation for a general view of the subject. The most simply organised Fungi known, are undoubtedly those which belong to the genus Torula. The well-known yeast-plant consists of a single ovoid cell, whose membrane is perfectly simple, and encloses a slightly granular, transparent fluid. It multiplies by the budding out of its membrane at one extremity into a projecting nipple, which soon becomes separated from the original cell by a constriction. As the newly formed germ enlarges, the constriction becomes more complete, and at last separation takes place. After the Torulæ, which are the only examples we are acquainted with of one-celled Fungi, come the innumerable *Hyphomycetes* or thread Fungi, so called because their reproductive, bears so small a proportion to their vegetative system, that it is in many cases altogether overlooked. The growing terminations of the mycelium filaments themselves become individualised, so as to form the germs, which separate from their parent cells by constriction, as above described in Torula. It is this acrogenous mode of spore formation which Schleiden considers as the character which distinguishes the true Fungi from the Lichens*; the latter developing "many spores simultaneously in the interior of a larger parent cell or ascus." Among the higher Hyphomycetes, however, the reproductive system appears in a more distinct and developed form. Thus, in Penicillium it consists of filaments which spring perpendicularly from the stroma, and are formed of elongated, club-shaped cells, joined end to end. These stalk-like filaments branch trichotomously in the most beautiful manner. From their extremities there spring others, which are much more slender, and consist of moniliform series of minute ovoid segments, separated from each other by constrictions, which are indistinct at the base of the filament, but become more and more complete towards its termination. At this point the segments detach themselves, and form the germs of the plant.† In other genera, the perpendicular sporiferous filaments are woven together into more complicated structures, the varieties of which it does not come within our present purpose to describe. As respects their component elements and the mode in which the spores are produced, they do not differ from those noticed above.

Fig. 141.



Branching sporiferous filaments of Penicillium verticillatum, about 150 *diam.* (Corda.)

34. The basidiosporous Fungi are characterised by the presence of a distinct membrane (hymenium), on the surface of which the spores are developed by a mode which, though it is still acrogenous, is considerably more complicated. The hymenium always consists of elongated pouch-like cells, arranged side by side, with their long axes perpendicular to its surface, and in close contact with each other. Some of these cells are longer than their neighbours, and from their free rounded ends, there emanate processes (usually four in number) in the form of pedicles. Upon the extremities of these are borne oval cellules, which, though in their earliest condition they do not exceed their pedicles in width, rapidly enlarge, and finally separate by a kind of constriction. In some basidiosporous Fungi, as in the Agarics, the hymenium is external, and its surface exposed to the atmosphere; while in others, as in the Gasteromycetes, it is internal, the spores being thrown, when detached from their pedicles, into one or more cavities enclosed in the substance of the receptacle. Of the last-mentioned division, we select a well-known genus (Geaster), for the purpose of illustration.

Fig. 142.

A basidium with its four basidospores, along with two other sterile basidia (*Geaster rufescens*), 300 *diam.*

* Schleiden places all the ascophorous Fungi among the Lichens. We shall find, as we proceed, that such an arrangement is altogether inadmissible. (Schleiden, Principles of Scientific Botany, p. 157.)

† Corda, Icones Fungorum, tom. i. p. 21.

35. At the period of the formation of the spores, the receptacle of Geaster (fimbriatus) is a solid body of a depressed spheroidal form. It presents for examination a central mass and a peridium, the tissue of the latter being continuous with that of the former only at the base. The central mass or kernel is originally

Fig. 143.

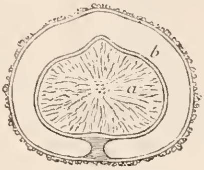


Diagram of receptacle of Geaster fimbriatus.

The kernel, *a*, is surrounded by its reticular membrane, which is indicated by the inner of the two double lines. The outer double line corresponds to the resistant external layer of the peridium. The intervening space, *b*, is occupied by a delicate tissue of spherical cells. At *c*, all these structures are continuous, as well with each other as with the mycelium from which the whole originates.

solid, but when fully developed, presents numerous irregular cavities, which are scattered through its substance. It is entirely composed, when in the solid condition, of delicate filaments similar to those of mycelium, the arrangement of which is as follows:—The superficial filaments are closely woven together, so as to form a delicate reticular membrane, which invests the whole kernel, and from the inner aspect of which a second and very numerous set of filaments passes off towards the centre. It is of these, or of their ramifications, that the corky, semi-elastic substance of the kernel is entirely formed. If we examine the cavities which have been mentioned as existing in the fully developed condition, we find that they are furnished with a

Fig. 144.

Section of a portion of the young receptacle of Geaster rufescens, about 100 *diam.*

The section has passed through one of the cavities, and shows the arrangement of the basidia which form its lining membrane. Some of these bear spores on their summits.

more or less continuous lining of basidia, bearing spores on their summits. These basidia have been shown, by careful observation, to be in fact the swollen terminations of the centripetal branching filaments above mentioned. The peridium it is less necessary to describe, as it has no immediate connection with the spore-bearing organs. It consists of an internal and an external layer, the latter being smooth and very resistant, while the former consists of delicate, transitory, spherical cells. In the ripe condition of the Geaster, the peridium becomes detached, at the same time splitting from apex to base in a remarkable and characteristic manner. Geaster may be considered as the type of a well-known family, including the *Lycoperdons, Bovistæ*, and others, all of which are characterised by the presence of a solid receptacle, furnished with numerous spore-bearing lacunæ. In almost all of these Fungi, the arrangement of the spores with their pedicles in relation to the basidia are the same, four pedicles emanating from each basidium. In the ripe condition the spores are always of a dark-brown colour, frequently approaching to black, and their surfaces are beautifully reticulated with linear furrows, between which there are little conical projections. Each spore possesses an external reticulated, and an internal homogeneous membrane. This last encloses a cavity, which is occupied by a fluid, which contains numerous oleaginous granules. The ripe spores, after their detachment from the basidia, lie loose in the lacunæ of the receptacle from which they are set free by the disintegration of the basidia, as well as of the filament with which they are connected. In this manner, in Geaster, the kernel is converted into a bag, formed of the delicate reticular membrane, described above as its proper investment. This bag contains a dark-brown diffluent mass, composed of the remains of the basidia and filaments along with ripe spores. Finally, the membrane gives way, and the spores are disseminated in the shape of a light, dry-looking powder.

36. We next pass to the consideration of the Fungi, among which the spore, instead of being produced at the summit of a basidium, or at the extremity of a simple filament, is formed in the interior of a vesicle or pouch, which is called a theca or ascus. Of these, the first which we shall mention belong to a group of subterranean plants, of which the truffle is the best-known example. The receptacle of the truffle consists of a fleshy mass, throughout which numerous sinuous cavities are interspersed. Each cavity is partly lined, partly filled with the thecæ and the cells upon which they are supported. This receptacle, like that of all other Fungi with which we are acquainted, originates from a pre-existing mycelium. In its unripe condition it displays on section a number of sinuous empty cavities, which either communicate with each other, or open at one or more points of the external surface. As the truffle advances towards maturity, the cavities are obliterated by the formation of a whitish tissue; so that on section, we observe the whole to consist of two substances—the one translucent, of firm con-

sistence and of a dark-brown colour; the other white and opaque. The former, which cor-

Fig. 145.

Section of part of the receptacle of a Truffle, about 250 *diam.*

a, outer layer of the peridium consisting of a resistant tissue of thick-walled cells; *b*, inner layer of the same, formed of filamentous tissue continuous with that of *v*, one of the venæ internæ, or partitions by which the compartments (originally cavities) of the truffle are bounded. Portions of two of these compartments are seen with the thecæ and septate filaments which they contain.

responds to the partitions which, in the young state of the truffle, separated the cavities, is continuous with the external tissue which composes the envelope or peridium, and constitutes the vena internæ of Vittadini.* The laminæ which it forms, consist of filaments running, for the most part, parallel to each other. The white substance which occupies the original cavities of the tuber, is formed of closed tubes, which are given off in great numbers from the surfaces of the laminæ. These tubes, which are the terminations of the filaments of which the laminæ are composed, are of two kinds. Some are of equal diameter throughout, and divided at intervals by septa; others, much shorter, are dilated at their extremities, and contain spores (thecæ). Each theca is an obovate vesicle, and contains two, three, or more spores, never more than eight. Each spore is invested with a beautifully reticulate, or sometimes warty epispore, within which may be distinguished a smooth inner membrane, immediately enclosing the oleaginous contents.†

37. The ascophorous Fungi are represented in their simplest form by the Uredineæ, a family which has been studied by numerous observers on account of the destructive properties of the plants belonging to it. The mass which is formed by the growth of the reproductive organs of Uredo under the epidermis of the leaves of the plants upon which it grows parasitically, may be aptly compared to a pustule, a grumous-looking substance, occupying, as it were, the place of the pus. On more minute examination of the cavity, we find that it is bounded by a kind of irregular wall or lining of pyriform cells, the smaller ends of which rest upon a reticular cushion of mycelium. These are probably the enlarged extremities of the mycelium filaments, with which many of them can be distinctly traced to be connected. Towards the base of the cavity other cells are developed, resembling those first mentioned in their general form, as well as in their relation to the mycelium. In these, however, the membrane is produced inferiorly, so as to form a tubular pedicle; while in the club-shaped upper extremity it is lined by a considerable deposit of granular protoplasma, so that here the central cavity is very much smaller than that of the external membrane. It is in this cavity that the spore is formed, at first not exceeding it in size, but afterwards increasing at the expense of the protoplasma, so as almost to fill the theca. In other genera, as in Phragmidium, there are pedicled cells of a similar form, and originating in a similar manner, which, however, instead of one spore, develop a number in their interior; these spores are arranged in linear series, and are formed in the same manner. The protoplasma, however, never disappears completely, but remains as a more or less consistent membrane, glueing the ripe spore to the spore-case which encloses it. Some of the Uredineæ possess a cyst which reminds us of the perithecium of the Sphœriaceæ, to which they are evidently closely related. The cyst is formed (Œcidium) of a single layer of roundish cells.*

38. From the Uredineæ we pass by a natural transition to the Discomycetes and Pyrenomycetes. These plants have been investigated with much success by MM. Tulasne, who have shown that they possess the closest relationship not only to the Lichens, but to the most simple thread Fungi. The very remarkable facts which these observers have discovered, render the study of these plants more satisfactory and instructive than that of any other family of the class. The Pyrenomycetes are represented by Sphœria, the receptacle of which consists, as is well known, of a spherical cyst, which is open above. Its wall is frequently prolonged upwards into a tubular beak, which projects beyond the surface of the bark or wood in which the whole plant is embedded. The membrane of the cyst (perithecium) is usually

* Vittadini, Monog. Tuberacearum, p. 2. et seq.

† L. R. & C. Tulasne, Histoire des Champignons hypogeés, 41-50.

* L. R. Tulasne, Recherches sur les Uredinées, &c. Ann. des Sc. Nat. 3me. S. t. vii. p. 12.

composed of polygonal, tabular cells ; it is lined by an inner layer, formed of the commencements of the paraphyses and thecæ, and of the filaments with which they are connected. The thecæ are obovate cells, the

Fig. 146.

Thecæ and paraphyses of Sphœria, about 300 *diam.*

membrane of which is of extreme delicacy. When fully formed, they contain from three to eight oval spores, the epispores of which are in the early condition delicate and pellucid, but by degrees become brown and opaque.

Fig. 147.

Ripe spores of Cenangium Frangulæ, 350 *diam.*

The contents of the spores, as is observed throughout the higher Fungi, consist of a fluid loaded with oily granules. The thecæ are arranged with their long axes perpendicular to the inner surface of the perithecium from which they spring, and are intermixed with a greater or less number of slender, cylindrical paraphyses. The whole perithecium is usually enveloped in the filamentous stroma or mycelium, from which it takes its origin. The Discomycetes are represented by the Pezizæ; between these and the Sphœriæ there are differences of external form, which, though they strike the superficial observer as important, are in reality trivial. While the receptacle of the Sphœria is a cyst with an apicial aperture, that of the Peziza is a cup-shaped disc, the concave surface of which looks upwards. This surface is lined with an ascophorous membrane, which resembles in every respect that of a Sphœria.

39. Along with the Pezizæ and Sphœriæ and those allied genera which resemble them in producing their spores enclosed in thecæ, there are other forms also included in the Pyrenomycetes and Discomycetes, which, while they resemble those last named in the general outline and structure of their receptacles, differ from them completely in the mode of origin of the spores. The simultaneous occurrence of some of these forms, along with their ascophorous analogues, or, in other instances, the successive development of both kinds of receptacles in the same position, had been frequently observed, and had given rise in the minds of some mycologists to the suspicion of the existence of a relation more close than was generally admitted. This suspicion did not, however, take a sufficiently distinct form to lead to observation until the MM. Tulasne, in a series of researches scarcely completed, showed that the genera in question, hitherto considered as distinct, were in fact identical, and that receptacles containing thecæ and paraphyses, are produced on the same stroma, or, in other words, on the same individual plant, as those which contain acrogenous spores.

40. The earliest researches of MM. Tulasne* were directed to the Pyrenomycetes. In some species of Sphœria, they found not only that the same stroma produces receptacles with acrogenous spores, which are followed by others bearing thecæ; but that, under certain circumstances, it may give rise to spore-bearing organs, of a much simpler character; viz. branching filamentous pedicles, bearing at their terminations single spores, and rising directly from the mycelium filaments, with which they are continuous. In this condition the plant cannot be distinguished from a thread Fungus, and has been hitherto described as such.

41. The later observations of MM. Tulasne † which are much more in detail, refer almost entirely to Discomycetes. In a species of Rhytisma, a genus of Discomycetes, which inhabits the epidermis of the leaves of plants, the stroma at first presents the appearance of a black spot of various extent on the surface of the leaf. In the substance of this stroma the first receptacles are formed ; they are cushion-shaped capsules, furnished with apicial apertures, like those of Sphœria, and are entirely occupied by a pulpy nucleus, which consists of slender branched filaments, often so long as to project considerably beyond the aperture. These filaments bear at their extremities innumerable minute linear sporules, which are enveloped in an abundant mucilage, and are expelled from the ripe capsules in the form of a long cirrhus. After the capsules which are developed during the early summer months have discharged their contents, they are succeeded by the lirelliform discs of the perfect Rhytisma. These do not arrive at maturity until the following spring, and bear

* Notes sur l'Appareil reproducteur dans les Lichens et les Champignons, Ann. des Sc. Nat. 3me. S. t. xv. p. 370.

† Nouvelles Recherches, &c. Comptes rendus, Séance du 13 Dec. 1852.

upon their upper surface thecæ and paraphyses like those of a Peziza. In other genera M M. Tulasne found that the ascophorous receptacles are preceded by capsules which produce, instead of the linear sporules above mentioned, cylindrical spores of a much larger size, each of which is supported at the extremity of a pedicle of its own.

42. Thus in the plants under consideration we find that, without counting the sporules which are produced by filaments rising directly from the stroma, there are no less than three varieties of spore-like structures which can be easily distinguished from each other. All of these may be produced upon the same, individual, and one instance is recorded in which a cupule of a Peziza was found, which bore among the normal thecæ, paraphyses with innumerable, slender, linear sporules at their extremities. As has been already hinted, the capsules which contain acrogenous spores, have been hitherto considered as belonging to genera distinct from those represented by the ascophorous receptacles with which they were found associated. The genus Cytispora is characterised by a structure which corresponds completely with that of the capsules described above in Rhytisma; and other genera as *e. g.* Sporocadus have a similar relation to the capsules, containing the larger variety of pedunculated, cylindrical spores.

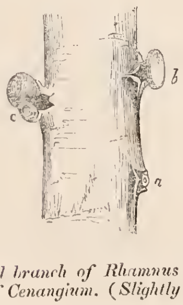
43. In order to facilitate the description of these various structures, a nomenclature has been devised by MM. Tulasne, which may be adopted with advantage. The minute, linear sporules, which are produced at the extremities of branched filaments, like the paraphyses of *Sphæria*, are called spermatia. The cylindrical bodies of much larger size, which are borne each at the extremity of a stipitiform cell, are named stylospores; while the term spore is reserved to those which are formed in the interior of a theca.

43. *bis*. In a third "Memoire" which has appeared since the above paragraphs went to press, MM. Tulasne have further prosecuted their researches on this interesting subject. The following is an abstract of their account of the development of a Pyrenomyces (Cenangium), which inhabits the bark of dead branches of the black alder (Rhamnus Frangula). The plant, in its natural position, is represented in *fig.* 148. The mycelium ramifies, in all directions, in the substance of the inner bark of the dead branch. From its filaments there spring, at irregular intervals, the receptacles, which as they develope, burst through the outer bark and epidermis and exhibit the various forms represented. The simplest variety (*fig.* 148. *a*) resembles in structure the organ described in § 49. as occurring in Scutula. In form, it is rounded, but at the same time somewhat conical. The stylospores (*fig.* 149. *a*) which it contains, are curved, crescentic bodies, supported on pedicles, which have an arrangement perfectly similar to that observed in Scutula. The receptacles or cupules in which thecæ are produced are deserving of great attention. In the early condition, their form is cyathoid (*fig.* 148. *c*), and they resemble those described (§ 41.) in Rhytisma. They contain at this time, innumerable spermatia (*fig.* 149. *b*), these being supported on filaments which spring from the inner surface of the cup, as well as of its margin. As the organ grows, it expands, and finally becomes discoid (*fig.* 148. *b*), when it possesses the structure

Fig. 149.

a, group of stylospores, with a fragment of the wall of the receptacle in which they are enclosed; *b*, similar group of spermatia. About 300 diam.

Fig. 148.



Part of a dead branch of Rhamnus Frangula, with receptacles of Cenangium. (Slightly magnified)

Fig. 150.

Vertical section of discoid receptacle of Cenangium, about 300 diam.

represented in *fig.* 150. The central portion of the disc is lined by an ascophorous membrane. The overhanging marginal fold still exhibits the filaments bearing spermatia, which characterised the earlier condition of the receptacle. Our authors are inclined to admit that the spermatia are to be considered as a male product, and the whole organ as analogous to a hermaphrodite inflorescence. The relative positions of the spermatia and thecæ seem admirably adapted to insure their contact with each other.

44. We now pass to the Lichens, with respect to which the greater part of our information is again owing to the researches of MM. Tulasne.* In these plants, as in the Fungi, the germination of the spore consists in the emission of a hollow filament from some part of its surface. This filament which is simply an extension of the spore-membrane, branches repeatedly and spreads over the surface, on which the spore has been sown; at the same time it divides by numerous septa, which occur at irregular intervals. By the intertwining of the resulting ramifications, a stroma is formed, to which the term hypothallus is applied, and which constitutes the vegetative system of the future lichen. So far the development is the same as the Fungi. At a longer or shorter period after the formation of the hypothallus, we begin to observe upon its surface a whitish layer of spheroidal cellules, intimately united with each other, as well as with the filaments from which they take their origin. This layer serves as the groundwork for a second formation of globular cells. These are distinguished from their predecessors, as well by the regularity of their form, as by the granules of chlorophylle which they contain. They are called gonidia, and are peculiar to the Lichens, among which their occurrence is almost constant.

45. Such is the origin of the thallus, which, although, at first sight, it appears to constitute the whole plant, forms only a part, and that not the most essential part of its vegetative system. In the Verrucariæ, the most simply organised Lichens with which we are acquainted, it does not attain to any higher development than that above described. The receptacles (apothecia), which closely resemble those of a Sphœria, are formed upon the surface of the hypothallus, which can only be distinguished from the stroma of the Fungus by the presence of scattered collections of gonidia. In the more complicated foliaceous Lichens, such as Parmelia, the mature thallus is formed of two kinds of tissues, the medullary and the cortical. The cortical tissue forms two layers — an inferior and superior — and consists of thick-walled cells intimately adherent to each other, and resembling those of analogous structure, which so often form the peridia of the higher Fungi. From the surface of the inferior layer are given off numerous laminar root-like

Fig. 151.

Vertical section of the apothecium of a Lichen (Parmelia aipolia) and of the subjacent tissue of the thallus, 200 *diam.*

a, Lamina proligera, consisting of thecæ and paraphyses; *b*, tissue of thick-walled cells continuous with the cortical tissue of the thallus. Subjacent to this, but separated by an irregular line of gonidia, is the medullary filamentous layer.

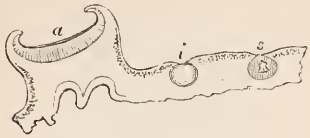
appendages. The medullary substance consists of a filamentous central layer, the elements of which resemble those of the hypothallus, and are directly continuous with them; on either side of this layer, between it and the cortex, or rather embedded in its substance, are the gonidia, which form a green tissue, distinguishable by the naked eye. To these a special function is assigned, which shall be noticed at the conclusion of the article under the head of Gemmation.

46. We have next to describe the receptacles, within or upon which the spores or spore-like organs (spermatia and stylospores) are produced. Of these there are three varieties, to which the terms *apothecia*, *spermogoniæ*, and *pycnides*, have been applied. The most common form of the apothecium is that of a *disc*, which may be plane, convex or cup-shaped. This form is that which characterises the *gymnocarpous* Lichens. In the *Angiocarpeæ*, the organ is closed upwards, its superior surface becoming internal, so as to form a conceptacle like that of the Pyrenomycetes, the form of which is subject to considerable variation. In either case, it is composed of two layers, the inferior or external, being formed of thick-walled cells which are soldered together, and resemble those of the epidermal layers of the thallus. The superior or internal layer is called the *lamina proligera*. It is formed of two kinds

* Mém. pour servir á l'Histoire organographique et physiologique des Lichens, Ann. des Sc Nat. 3me S. t. xvii. pp. 5. and 173.

of elements: first, the *paraphyses*, which are linear, claviform filaments, composed of from

Fig. 152.



Section of fruitful thallus of Sticta pulmonacea, about 20 diam.

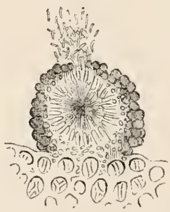
a, discoid apothecium. The vertical lines indicate the lamina proligera; *s*, spermogonia containing spermatia; *i*, empty spermogonia.

six to eight cylindrical cells, joined end to end; and secondly, the *thecæ*, which are obovate vesicles, each containing, almost invariably, eight spores. These elements are arranged side by side, their long diameters being perpendicular to the surface of the apothecium. They appear to be glued together, even in the fully formed apothecia, by an intermediary gelatinous substance, which, however, there is good reason for supposing to be nothing more than a thickening of the external membrane, from which it cannot be distinguished, either in respect of its chemical or other characters. Iodine colours this substance, as well as the external membranes of thecæ and paraphyses, blue, without the addition of sulphuric acid. In the early condition, the cavities of the thecæ are occupied by a yellow, plastic material, out of which the spores are afterwards formed. The thickness of the external starchy membrane is at this period relatively more considerable than later; as the spores increase in size, it gradually diminishes. The structure of the fully formed spore is best observed in those species in which it is largest. The spore-membrane, of considerable proportional thickness, is smooth and semitransparent, wholly unaltered by iodine and sulphuric acid. The contents consist partly of mucous granules, which are coloured brown by iodine, partly of yellowish oil globules. The whole is usually invested, even after its escape from the theca, with the still adherent remains of the inner protoplasmic layer, by which it was immediately surrounded. In form, the spores are most frequently ellipsoid and unilocular. In other instances, however, they are divided by one or more partitions. This division is either complete, so that the spore resembles two obovate cells joined by their larger ends; or incomplete, the septa being in some cases scarcely distinguishable from the protoplasmic contents of the central cavity.

47. The spores are discharged from the thecæ with an elastic force often sufficient to project them to a considerable height above the surface of the apothecium; a fact, which M. Tulasne seems to have shown to be dependent on the great capability of imbibing moisture possessed by the lamina proligera, which much exceeds that of the tissue immediately subjacent. It resembles altogether what is observed in the Pezizas, whose spores, it is well known, are projected with such force as to form a cloud above the receptacle.

48. We have next to notice the remarkable organs which Itzigsohn* described as the antheridia of the Lichens, and to which he was the first to assign a distinct function. They had been previously adverted to by several botanists, and had been usually considered as parasitical Pyrenomycetes, which they closely resemble. They consist of conceptacles embedded below the upper surface of the thallus; their presence is revealed by the appearance of blackish, projecting points, scattered at irregular intervals. The form of these organs,

Fig. 153.



Spermogonia of Scutula Wallrothii, 150 *diam.*

The spermatia are seen escaping in numbers from the apicial aperture of the organ.

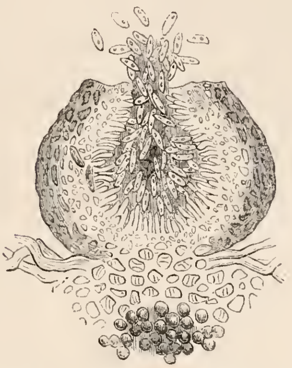
which MM. Tulasne have named spermogoniæ, is globular, ellipsoid, or oblong. Their external envelope is frequently hard and crustaceous, and usually blackish. The cavity may be simple or multiple; in the latter case all the compartments or sinuses open at one ostiole. The whole of the cavity is occupied by a filamentous tissue, which consists of two elements — viz., spermatia and the organs on which they are supported. The latter are simple or branched filaments, which are usually undivided, but occasionally jointed. They originate from the inner surface of the conceptacles. At their summits and articulations, they bear the spermatia, which are straight or curved linear organs of great tenuity, and are motionless. They are coloured brown by iodine; both the spermatia and filaments are embedded in an abundant mucilage; many of the former are sterile, and are so long that they project beyond the opening of the conceptacle like a kind of cirrhus. The whole structure corresponds in every respect with that of the spermatia-bearing conceptacles of the Discomycetes and Pyrenomycetes.

49. To a third variety of conceptacle, M M. Tulasne have assigned the title of pycnidis, This organ, although it has only been observed in two genera, Abrothallus and Scutula,

* Bot. Zeitung. 1850. S. 913.

is no less important, as forming another connecting link between the Lichens and Fungi. The special characteristic of these organs is to be found in their containing, instead of thecæ or paraphyses, stylospores, supported on stipitiform pedicles or basidia. In their

Fig. 154.



Pycnidis of the same, about 150 *diam.*

The stylospores are escaping from the upper orifice of the organ. (The figures from 143 to 154 inclusive, are after Tulasne.)

general form they resemble the spermogoniæ, but their walls are thicker and they are larger. Like them they are provided with a vertical ostiole. The stylospores are oblong, cylindrical bodies, more than twice the length of the spermatia (from $\frac{1}{2000}$ to $\frac{1}{1500}$ of an inch), obtuse at both ends, very slightly curved, colourless, and containing only granular protoplasma. They are supported on pedicles, which have the same arrangements as in the spermogoniæ. They are simple, linear tubular filaments, which taper towards their extremities. Just as the spermogoniæ correspond to the spermatium-bearing organs of the Fungi, the pycnides correspond to those receptacles, containing stylospores, which we have had occasion to describe both in the Discomycetes and Pyrenomycetes.

50. *Summary.*—The reproductive organs of the Fungi and Lichens are of five kinds:—1. Sporules, which are formed by the constriction and subsequent separation of the extremity of a simple cylindrical filament; 2. Spermatia with their supporting pedicles; 3. Stylospores, with their styles; 4. Thecæ or asci; 5. Basidia, with their basidiospores.

Of these the last mentioned are to be found only, as we know at present, in Fungi which are provided with no other reproductive organ. The first four, on the other hand, all of them occur in plants belonging to one family of Fungi—viz. the Disco- and Pyreno-mycetes: they also all occur, with the exception of the first, among the Lichens. They may be arranged, as regards the complexity of their form and structure, in the order in which they are placed above, the simple acrogenous sporule standing first. A similar arrangement may also be adopted in the description of the corresponding varieties in the reproductive phenomena which manifest themselves in connection with each variety of spore-like body. As regards the first of these, nothing further need be said, as the formation of the sporule by division, as described above, constitutes the whole reproductive process. It is exemplified in the stroma of a Sphœria, when in a condition corresponding to that which characterises a Melanconium. The spermatium is found only in a special receptacle, the general form and structure of which remain always the same, as in the Cytispora-like capsule of the Disco- and Pyreno-mycetes and the spermogoniæ of the Lichens. The stylospores are also formed in special organs (pycnides, and the corresponding organs among the Fungi), which differ from the last only as regards the structure of the parts upon which the spore is immediately supported. Lastly, the receptacles which bear thecæ are of larger size, more complicated in their structure, and later in making their appearance than any of the rest, as in the instance of the disc of Peziza, the closed receptacle of Sphœria, and the apothecium of the Lichens.

51. The Pyreno- and Disco-mycetes are, as we have seen, so closely allied to the Lichens as regards their reproductive organs, that the characters of the two families seem in this respect to merge into each other. The distinction is to be sought in the vegetative system. The thallus of the Lichen differs from the thallus-like stroma of the Fungus in its possessing two additional elements, the cortical layer and the gonidia. We observe their first appearance in the most simple form in Verrucaria.

52. There is as yet no sufficient ground for definitively concluding that the reproductive functions of the asci and spermatia are complementary to each other; or, in other words, that these organs are sexual. There is, however, good reason for considering it probable; first, because, when spermatia and asci are produced on the same *mycelium*, the former always precede the latter in their development by a considerable period, just as among the higher Cryptogamia, the antheridia precede the archegonia; and, secondly, because the organs on which the spermatia are supported, and the asci, stand in an anatomical relation to each other, and to the receptacle within or upon which they are formed, which closely resembles those of the antheridia and epispores of the Fuci, or of the antheridia and tetraspores of the Florideæ. We are well aware that these analogies do not afford the slightest proof of an actual correspondence between the organs in question. All more direct evidence, however, is absent; no observations have been made to show that the spermatia or stylospores exercise any influence on the thecæ or their contents, and on these important points, therefore, we must look to further ob-

servations for the grounds on which an opinion may be formed.

53. The fifth and last variety of reproductive organ mentioned above, is the basidium. The Mushrooms, along with another group of Fungi, which is distinguished by the possession of loculate receptacles, each loculus of which is lined with a hymenium, as *e.g.* Lycoperdon, include nearly all of the genera in which it occurs, and form Leveillé's order, Basidiosporeæ. The order is a very natural one, and between it, and any of those which are most closely related to it, we can find no intermediate forms which at present might serve as guides in comparing the reproductive organs of the one with those of the other. The basidiospore is distinguished from all the other acrogenous forms (stylospores, spermatia), by well-marked and easily-defined characters—viz. first, by its much greater complexity of structure; and, secondly, by the very peculiar and uniform arrangement, according to which the spores are developed in fours at the summits of the *basidia*.

Second Part.

Higher Cryptogamia and Phanerogamia.

54. In the attempt which we have made in the preceding sections to discover the order of succession in which nature has arranged the various families included among the Algæ, Fungi, and Lichens, we have encountered difficulties at every step. The extension of the same inquiry to the higher Cryptogamia and Phanerogamia is much more satisfactory in its results. "The comparison of the history of the development of the leafy Mosses and Hepaticæ on the one hand, and of the Equisetaceæ, Rhizocarpeæ, and Lycopodiaceæ on the other," says Hofmeister, "has shown the most complete correspondence of the formation of the fruit of the one with the formation of the embryo of the other. The *archegonium* of the Mosses, the organ within which the rudiment of the fruit (Fruchtanlage) is formed, has a structure altogether similar to that of the archegonium of the Ferns (in the widest sense)—to that part of the prothallium in whose interior the embryo of the frond-bearing plant originates. In both of these large groups of the higher Cryptogamia, we have a single cell, originating freely within the larger central cell of the archegonium, by the constantly repeated divisions of which, in the Mosses, the fruit—in the Ferns, the leafy plant, takes its origin. In both cases the division of this cell fails to take place, and the archegonium aborts, if the spermatic filaments (Saamenfäden) do not reach it at the moment that its summit gives way." *

55. The higher Cryptogamia and Phanerogamia form a series, which, commencing with the frondose or membranous Hepaticæ, ascends through the Jungermanniæ and Marchantiæ to the true Mosses. At this point, the thread is interrupted, but is easily resumed, and followed through the Ferns and Lycopodiaceæ to the Rhizocarpeæ. Between these last and the Phanerogamiæ, there is again an interval of obscurity, which is succeeded in the latter by a new order of phenomena. The plants belonging to the series before us are characterised by their displaying a regular alternation of two generations which differ widely in their organisation. Of these, the first, taking its origin from the germinating spore, develops two kinds of organs, the reproductive functions of which are complementary to each other. One of these (archegonium) is destined for the reception of a germ-cell, while the other (antheridium) sets free a number of corpuscles closely resembling the antherozoids of Chara, which have been already described. It is from this germ-cell that the second generation commences its existence; its development being, as there is now every reason to believe, dependent on the actual contact of the antherozoids. It differs completely in form and structure from its parent, and possesses only one kind of reproductive organ. This organ throws off germs (*spores*), each of which is capable, independently of any external influences, except those of heat and moisture, of transforming itself into a new individual. This in its turn produces *pistillidia* and *antheridia*, and thus forms the starting point of a new development.

56. Supposing the history of the development of the plants under consideration to commence with the germination of the spore, and terminate with its arrival at maturity, it may be divided into two periods. Of these the first is completed in the full development of the archegonia and pistillidia, and the combination of their products, so as to form an embryo; while the second terminates in the full development and distribution of the spores.

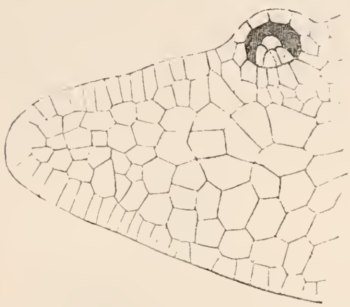
57. Among the lower Hepaticæ, the vegetative system (*frond*) consists of a simple membranous expansion, which may be considered equivalent to what would result from the soldering or fusing together of the leaves and stem of a more highly developed plant. The frond is of various forms—always originally linear, and lengthens at one (the anterior) extremity only. At the other end, which is earliest formed, cessation of vegetation, and marcescence are constantly taking place. The adult plant assumes very various forms, which arise from the repeated bifurcation of the original riband-shaped shoot. In the plant, the development of which we are about to describe (Anthoceros lævis) as one of the most simple of the Hepaticæ in its structures, the fully-formed frond is a lobed expansion of succulent, dark-green parenchyma, the general contour of which is circular. We shall divide the history of its development into two periods, corresponding with those laid down in the last paragraph.

* Hofmeister, Vergleichende Untersuchungen der Keimung, Entfaltung u. Fruchtbildung höherer Cryptogamen. p. 139. Leipzig, 1851.

58. *First period.** — *From the germination of the spore* arises a tubular filament, which is converted directly, by successive divisions, into a simple riband-like frond, with a notch in its anterior margin, containing a young shoot. At whatever age the plant be observed, the actively growing portions are shoots which resemble the spore plant in form and structure, and it is at various points of the upper surface of these shoots that the reproductive organs are developed.

59. *The development of the antheridia* commences in the still very young shoot, by the separation "of a circular group of about sixteen of the superficial layer of cells from those of the tissue below it. There results a small lentil-shaped lacuna in the parenchyma, which

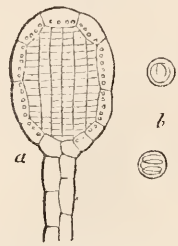
Fig. 155.



Section of young shoot of Anthoceros levis, passing through the lacuna in which the antheridia are developed. The rudiments of the antheridia springing from its floor, project upwards into its cavity. 50 diam.

is filled with watery fluid, and roofed over by the cellular layer above mentioned." Each of the cells forming the floor of the lacuna, is divided by two septa, one parallel to the axis of the frond, and perpendicular to its surface, the other also perpendicular, but cutting the first at right angles. The membrane of each of the resulting small cells buds out upwards, so as to project into the lacuna, and soon after, the upper projecting portion is cut off from the rest by a transverse septum, and becomes the parent cell of the antheridium. A second septum is then formed above the first, and parallel to it. This is succeeded by a third, which is inclined to the horizon at a small angle. Above it is a fourth, similarly inclined, but in the opposite direction; next follows a fifth, parallel to the third, and so on alternately. In this manner is formed a cylindrical papilla, consisting of two vertical series of cells, each of which is a segment of a cylinder. Each is next bisected by a radiating vertical septum, so that the papilla is now formed of four instead of two vertical columns. The penultimate cell of one of these columns next divides by a vertical septum, parallel to a plane touching the centre of its outer surface. This meets the perpendicular wall last formed at 45°, and divides the cell into an external tetrahedral, and an internal three-sided compartment. The latter divides twice by septa, which cross each other at right angles, so as to form a central group, which, as it rapidly enlarges, causes the four less actively growing cells by which it is surrounded to assume a tabular form. In its further development it is converted into a mass of very numerous and minute regularly-arranged tessellar cells, in each of which is found "a lentil-shaped vesicle which occupies the greater part of its cavity." Shortly before the antheridium arrives at maturity, the membrane of the cells disappears; the vesicles float free, and there is now found rolled up in each, a spiral fibre of from 2½ to 3 coils, which is coloured yellow by iodine. The ripe antheridium presents the general form and appearance shown in fig. 156. The cellular mem-

Fig. 156.



a, diagram of antheridium of the same, 250 diam.; *b*, lenticular cellules containing antherozoids, 600 diam.

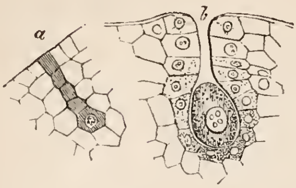
brane, resulting from successive division of the four cells, which originally surrounded the central mass, gives way at the apex of the organ. In the meantime, the layer of cells which roofed over the lacuna has split open. The escaped spiral filaments (antherozoids), as seen under the microscope, soon after lose the vesicles in which they were enclosed; "each slowly revolving round its own axis, lazily progresses in the surrounding water."

60. *The development of the archegonia* in Anthoceros differs from that of all other Hepaticæ in its much greater simplicity. A single row of cells commencing at the upper surface of the young shoot, and directed towards its interior, becomes distinguished from those surrounding it by the quantity of granular mucus which it contains. The lowest cell of the series becomes larger than the rest. In its interior a daughter cell (germ-cell) which nearly occupies its cavity, is formed around a pre-existing central nucleus. The contiguous walls of the cells forming the remainder of the series are absorbed. Hence results a canal which leads from the surface to the cavity of the basal cell. It is difficult to believe that an arrangement so remarkable can have any

* The following description is abridged from Hofmeister in *loc. cit.* pp. 4—9.

other object than the admission of the antherozoids.

Fig. 157.

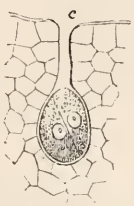


Archegonium of the same, 300 *diam.*

a, origin of the archegonium; the shaded vertical row of cells constitutes the rudiment of the organ; *b*, archegonium immediately before impregnation.

61. *Second period.—Fructification of the archegonia.* In the greater number of archegonia, development ceases at the point above described. In those in which the germ-cell has received the influences necessary for its fructification, this last-named body enlarges rapidly, and very soon divides by a slightly

Fig. 158.

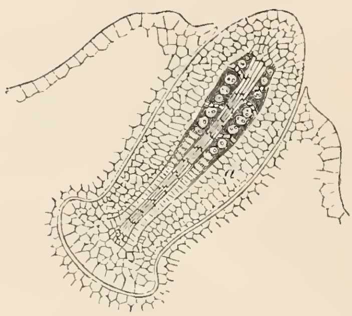


Archegonium of the same immediately after impregnation. The germ-cell has divided by an oblique septum.

oblique septum, which is followed by a number of others, alternately inclined in opposite directions. This results in an egg-shaped body, perfectly separable from the surrounding tissues. The last-formed summit-cell now divides by a septum which is inclined not in the opposite direction, but in a direction at right angles to that of its predecessor. This is followed by a second in the same relation; that by a third, and so on continuously. The cylindrical rudiment now consists of four columns of cells, each of which is divided symmetrically by a vertical septum, into an external trapezoid and an internal three-sided cell. The former again divides, first, by a vertical, then by a horizontal septum, both of them perpendicular to the surface of the rudiment, which now consists of four central cellular columns, which are enclosed in eight others formed of trapezoidal cells. These last divide by vertical septa, alternately parallel and perpendicular to the external surface, by means of which the rudiment gradually thickens. This process goes on much more actively at the lower than at the upper or middle portion, in consequence of which it becomes club-shaped; its swollen base being embedded in the parenchyma of the stem of the parent, and causes absorption of its cells. The cells in the neighbourhood of the originally six-sided canal leading to the germ, have in the meantime rapidly multiplied. The upper part of the canal now encloses the growing extremity of the rudiment, which, however, is separated from it by a quantity of fluid. It opens at the apex of a nipple-shaped projection of the upper surface of the frond, by a narrow aperture through which the conical upper extremity of the rudiment protrudes, and, as it rises, usually carries with it the remains of the cells immediately surrounding the narrow channel through which it has forced its way. It now presents the horn-like form, characteristic of the mature fruit, from which the generic name of Anthoceros is derived.

62. *Changes preparatory to the development of the spores.*—An axile cylindrical column, consisting of four cellular piles, becomes distinguished from those surrounding it by the cessation of the division of its cells by horizontal septa. In the layer which immediately surrounds it, on the contrary, division by horizontal septa occurs twice as frequently as in any other portion of the fruit. The hitherto homogeneous parenchyma becomes in con-

Fig. 159.



Section of half-ripe fruit of the same, 120 *diam.*

The axile column of elongated cells is the columella. Next to it are two dark spaces corresponding to a cavity, which contains at its upper part parent cells of spores and elaters,—inferiorly the tubular cells from which they originate; *a*, capsule.

sequence distinguishable into three portions — an external, of about five concentric layers of trapezoidal cells (the future capsule), an axile portion of elongated columnar cells (the future columella), and, interposed between these, a single layer of tabular cells, whose greater surfaces are horizontal (the cells from which are formed the spores and elaters).

63. *Development of the spores.*—Those of the cells last mentioned, which are destined to become the mother-cells of spores, soon become detached from their neighbours, and assume a spherical form. Each at first contains a large central nucleolated nucleus, and

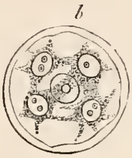
a quantity of granular mucus. Soon this last arranges itself in two masses, at opposite

Fig. 160.

Original parent-cell of spores of the same, 500 *diam.*

sides of the central nucleus. Each of these masses is transformed into a new nucleus, from which radiating threads of mucus stretch to the internal surface of the corresponding half of the cell. Each new nucleus is, when fully formed, vesicular, possessing a membrane of extreme delicacy, and is surrounded by a layer of protoplasma. At a later period its contour becomes cloudy and indistinct; this change being preparatory to a second division, which results in the formation of four new nuclei similar to the first two; these

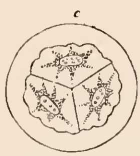
Fig. 161.



The same, containing four vesicular nuclei,

soon place themselves in such a manner, that each would occupy one angle of a regular tetrahedron contained in the parent cell. Up to this point the original central nucleus has remained; it now disappears, and six septa are formed simultaneously, which radiate from the centre to the circumference, one between every two nuclei, in such a manner as to divide the parent cell into four compartments, which are the special parent cells of the spores.

Fig. 162.



The same, divided into four compartments.

(The above, from 155 to 162, inclusive, are after Hofmeister.)

In each new cell, after this wall has become thickened by the deposition of a gelatinous material on its inner surface, a spore is formed, which, even at the first appearance of its membrane, occupies the whole cavity. As it approaches maturity, it assumes a brownish yellow colour, its external surface remaining perfectly smooth. In those of the cells of the middle layer of the half-ripe fruit, which are destined to the formation of the so-called elaters, the tubular form is permanent. In each cell the nucleus disappears, and is replaced by two others, between which a perpendicular septum is formed. From a repetition of the same process, there results a cylindrical body consisting of a series of four cells, the fully formed elater.

64. No sooner are the spores of the upper part of the capsule ripe, than it splits into two valves; dehiscence commences at the apex, leaving, as it proceeds, the columella with the loosely attached spores and elaters.

65. *Jungermanniæ frondosæ.*—From Anthoceros we pass to a group of plants, which, while they resemble it in their mode of growth, differ from it considerably in the form of their antheridia and archegonia, and still more in that of the organs in which they are contained. Here as in Anthoceros we follow the description of Hofmeister (Pellia epiphylla).*

66. *First period.—Germination of the spores.*—The spore is an ovoid cell, divided into four by three transverse septa, and enclosed in a finely granular external membrane. Of the four cavities, one of the terminal ones distinguishes itself from the rest by the small quantity of chorophylle which it contains. This cavity, or rather the cell which it represents, develops in germination, to the first hair-like roots; while the others, by successive divisions by septa in the direction of the long axis of the spore, form the rudimentary flattened stem of the young plant.

67. *The antheridia.* — The rudiments of the antheridia make their appearance as club-shaped projections of the upper surface of the young spring shoots. Each such projection originates from a single cell of the superficial layer by a mode of division which corresponds in every respect with that described in Anthoceros (§ 59). The completely formed antheridium consists of a globular mass of very small four-sided tessellar cells, which is surrounded by an outer layer of about twenty flattened cells, containing chlorophylle granules in contact with each other by their margins; the whole is supported on a very short stalk, consisting of only four cells. Each of the small cells contains a lentil-shaped vesicle, within which a spiral fibre is rolled up. This fibre moves with great activity for about ten minutes after its escape, revolving round its own axis, and at the same time progressing rapidly. The posterior extremity is slightly thickened, while from the anterior which tapers off gradually to a point, there emanate two long and delicate cilia, like those of the antherozoids of Chara. These, as well as the slender prolongation of the tail, manifest an active "winding screw-like" motion. These phenomena remain in perfection only for about ten minutes after the escape of the filament.

68. *Archegonia.*— The rudiments of the archegonia make their appearance as oval cellular bodies (from four to twelve in number) in the notch, which in Pellia, as in other frondose Hepaticæ, is found in the anterior margin

* Hofmeister, *loc. cit.* pp. 10—20.

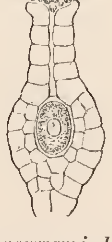
of the young shoot. Soon after their origin, there is formed, by the continued growth of

Fig. 163.

Antherozoids of Pellia, 400 *diam.* (Thuret.)

the shoot below them, a thin laminar prolongation upon the surface of which they are supported. By a process of cell-division resembling that observed in the development of the antheridia of Anthoceros, each rudiment is converted into a cylinder, rounded above and consisting of a single central cellular column, surrounded by a single layer, which is formed of four perpendicular series of flattened cells in contact with each other by their edges. The cells of the central column contain granular mucus, in which vesicular nuclei are embedded. As the archegonium becomes fully formed, the lowest cell in the series, as well as its nucleus, enlarges, and the cells of the outer wall in its neighbourhood rapidly multiply, so that the organ becomes swollen out at its lower part. The development is completed by the disappearance of the transverse septa, which separate the cavities of the cells forming the central column. In this manner is produced an axile channel, closed above, and terminating below in a flask-shaped dilatation, in which

Fig. 164.



Archegonium of Jungermannia bivaricata at period of impregnation, 400 *diam.*

Cellules containing antherozoids are observed at the entrance of the canal.

the enlarged nucleus of the basal cell (germ-cell) is contained. Soon the cells forming the summit of the archegonium give way, so as to open a communication between its cavity and the external atmosphere.

69. *Second period.—Development of the embryo.*—In consequence, as there is every reason to believe, of the entrance of the spiral filaments into the cavity of the archegonium, the germ-cell is divided by a tranverse septum into a larger inferior and smaller superior (hemispherical) portion. This last next divides by two perpendicular septa crossing each other at right angles, which are succeeded by a third, which is horizontal. This is succeeded by others parallel to it, each new septum being placed immediately above its predecessor. Hence results a cellular cylinder, the rounded summit of which always consists of four cells, divided from each other by crucial septa. By successive cell-divisions, this body becomes a pear-shaped cellular mass. Afterward by the lengthening of its middle third, the cylindrical stalk of the perfect fruit is formed, and still later from the lower third springs a cup-shaped sheath, the margin of which reaches to about a third of the length attained by the stalk of the fruit before it has escaped from its calyptra.

70. *Changes preparatory to the development of the spores.*—At an early period, when the young fruit is still pear-shaped, its rounded upper end (the future capsule) manifests peculiarities in its intimate structure. The cells of its superficial layer are divided repeatedly by septa perpendicular to the surface, while those which they enclose gradually enlarge without dividing. The result of this process is the formation of a central mass of large dodecahedral cells (parent cells of the spores and elaters), which is surrounded by a single layer of tabular cells of not more than a quarter their breadth (the future wall of the capsule). As the development proceeds, the walls of the central cells become thickened by the deposit of a gelatinous material on their internal surfaces. This material, which is coloured violet by iodine, swells out, and finally dissolves, on the addition of water, the globular primordial vesicle, which occupies the centre of the cells, being brought into view. Still later both the cell membranes and their gelatinous linings disappear, and the primordial membranes are left, lying in the cavity of the young capsule. Soon after they clothe themselves with new membranes of cellulose, and assume forms, which differ according as they are destined to become parent cells of spores or elaters. Those of the newly formed cells which are to be elaters, assume the form of spindles. They are found partly grouped round the axis of the capsule, partly in series which radiate from it towards the circumference. The future parent cells retain only for a short time their globular contour: soon four projections of the membrane of each cell become visible, each of which would correspond in position to one of the angles of a regular tetrahedron contained in the parent cell. These projections increase so rapidly, that in a short time the whole presents the appearance of four egg-shaped

sacculi blended together by their smaller ends in such a manner that their axes meet at a central point, each forming with all the rest angles of 120°. The cell-wall now becomes thickened by the deposition of a granular material on its inner surface, which takes place most rapidly along the linear ridges which separate the sacculi. In this manner six imperfect dissepiments are formed, which stretch from the ridges towards the centre, and encroach so far on the central cavity, that it now communicates with the cavities of the sacculi only by four narrow circular channels. These changes are followed by the formation in each sacculus of a delicate vesicle (the spore) completely filling the cavity of each. No sooner has this taken place than those portions of the parent cell which correspond to the sacculi dissolve and disappear, the four oval spores remaining attached for several days to the still permanent tetrahedral central portion, which consists of vitreous cellulose. The central nucleus of each spore now disappears, and is replaced by two others, around which the mucous and chlorophylle granules group themselves. A septum is soon after formed between them, dividing the spore into two halves, in each of which the process is repeated. In the meantime the coloured external membrane is secreted on its external surface. The ripening of the capsule and consequent scattering of the spores takes place in spring, a year after the development of the archegonium within which the fruit originated.

71. Our limits will not permit us to enter upon the history of the development in other families of Hepaticæ. In the higher Jungermanniæ, which are provided with a distinct stem, as well as with regularly formed and symmetrically arranged leaves, it closely corresponds to that of Pellia. In the Marchantias, in which we have again a frondose stem, we have considerable differences. The antheridia are found on special receptacles of various forms, sometimes stalked capitula, concave superiorly, like the stalked apothecia of some Lichens (Marchantia polymorpha), sometimes sessile. However much the general form may vary, they agree in their relation to the antheridia. These last are flask-shaped bags, and always completely immersed in the parenchyma subjacent to the upper surface of the receptacle. This surface is always found to be scattered over with nipple-shaped elevations. At the summit of each an aperture is observable—the termination of the long and narrow neck by which the cavity of the antheridium communicates with the surrounding medium. The fully formed antheridium consists of a central mass of quadrangular cells, which, surrounded by a single layer of others much larger and of a tabular form, is continued upwards so as to form the narrow neck; the whole being closely invested by the parenchyma of the receptacle. Within each of the central cells is found a lentil-shaped vesicle containing a spiral filament, which only differs from those described already, in its greater minuteness. The archegonia of Marchantia are produced on the under surface of a somewhat umbrella-shaped, deeply lobed, stalked receptacle. This body corresponds in the mode in which it takes its origin from the notch in the anterior margin of the frond, with the ordinary vegetative shoot, of which it is obviously a modification. Its development has been well described by M. Mirbel.* The structure of the archegonium, and the commencement of the development of the fruit, correspond very closely with what has been described in Pellia. The mode of formation of the spores and elaters differs, however, considerably. The latter, which in the last-named plant, are nothing more than fusiform septate cells, attain in Marchantia, as well as in many Jungermanniæ, a more complicated structure. Their development has been described in an admirable contribution by Mr. Henfrey, who finds that the young elaters are, like those of Pellia, elongated fusiform tubes, and contain at first only colourless protoplasma.† Soon after starch granules are deposited in their interior, and they are converted by a growth which is much more rapid in length than in breadth, into very slender, hollow filaments, attenuated at each closed extremity. Still later, the starch and protoplasma disappear, and at length faint streaks, denoting the nascent fibres, are to be perceived upon the walls. These become gradually more and more distinct, till, in the mature elaters, they present themselves as strong flattened bands. In Marchantia there are two fibres, which coil in opposite directions, and are confluent by their ends at the extremities of the tubes in which they are contained. At the time of the scattering of the spores the cell-membrane gives way, and the elastic fibre rapidly uncoils, at the same time lengthening considerably. The parent cells of the spores in Marchantia are also, at an early period, fusiform. They are arranged side by side with the young elaters, from which they differ in being very much broader. Each of these cells is converted, by the formation of transverse septa, into a series of four, which afterwards separate from each other. In each of the new cells, the protoplasma increases in quantity and assumes a yellow colour. Still later it begins to accumulate into four distinct masses, each of which becomes invested in a cellulose membrane, and, after the solution of the membrane of the parent cell, assumes the structure and appearance of the ripe spore.

72. *Mosses.*—The Mosses are distinguished from the leafy Hepaticæ, first, by differences in the structure and arrangement of the stem and leaves, involving greater complexity; secondly, by the fact that the leafy axis is not developed directly from the spore, but, with the intervention of a confervoid structure (proto-

* Recherches Anat. et Phys. sur le Marchantia, Mém. de l'Acad. v. xiii. p. 380.

† Transactions of Linnæan Society, vol. xxi. p. 106.

nema),* resembling in all its relations to the future plant, the mycelium of the Fungi and Lichens.

73. *First period.—Germination of the spore.*† —The spore of the Mosses is a nucleated cell, the solid contents of which are granular, and consist of protein compounds, starch and dextrine. From the budding out of its membrane, results a hollow filament, which, as it lengthens, divides by a succession of transverse septa. It then begins to branch in all directions, each branch resembling the parent, and ramifying in the same manner. Hence results an entangled network of filaments of a brilliant green colour, which spreads over the moist surface on which the spores have been sown. At length some of the filaments are observed to give off lateral branches which differ from those previously formed in being more slender and containing less chlorophylle. In some of these the terminal cell, after dividing four or five times, becomes globular, and is transformed into the rudiment of a leafy axis.

74. *Development of the antheridia and archegonia.* — These organs are usually found in groups, which are situated either at the termination of the stem or branches, or in the axils of the leaves. In either case they are surrounded (with the exception, in many genera, of the axillary antheridia) by special arrangements of modified leaves (involucres). Those involucres which surround the antheridia are called perigonia, and are composed of leaves much smaller than the ordinary leaves of the stem. Those leaves which enclose the archegonia, small at first, attain a large size as the fruit approaches maturity. In some (hermaphrodite) mosses, both antheridia and archegonia are contained in one involucre.

75. In the very diminutive plants belonging to the genus Phascum, which we select as examples on account of their great simplicity of structure, the groups of archegonia are terminal, those of antheridia usually axillary. The growing extremity of the stem (terminal bud) or axillary bud, when destined to bear reproductive organs, instead of developing to a new axis, becomes flattened in such a manner as to present a slightly convex disc, which takes the place of its conical growing extremity. It is upon the surface of this disc that the rudiments, whether of antheridia or of archegonia, originate, by a process precisely similar to that which we have described in the commencing development of the antheridia of Anthoceros. The rudiment consists, as in Anthoceros, of four columns of cells, combined so as to form a cylindrical club-shaped body. The development and ultimate form of the archegonium corresponds so completely with what has been described in the Jungermanniæ, that it is unnecessary to describe it. The fully formed antheridium of Phascum is a club-

Fig. 165.

Section of termination of fruitful stem of Phascum cuspidatum, 50 *diam.*

On the right a female, on the left a male inflorescence. From the slightly convex surface which forms the summit of the stem, spring in the one case the archegonia, in the other the antheridia, along with numerous jointed filaments.

shaped body of about the same length as the archegonium, and consists of a central mass of minute quadrangular cells, which is enclosed by a single layer of tabular cells, in contact with each other by their edges. Shortly before the antheridium arrives at maturity, the quadrangular cells, each of which contains a spiral filament enclosed in a lentil-shaped vesicle, are dislocated. This is followed by the total disappearance of their membranes, so that the vesicles float free in the cavity of the now ripe antheridium. No sooner is this the case than the organ gives way at its summit, and discharges its contents in the form of an intestine-like coil of mucus, consisting of the lenticular vesicles with their contents. Soon after, this is dissolved, and the spiral filaments commence their active motions.

76. *Development of the fruit.* — The early stages correspond with those described in Pellia. At a period when the lower dilated portion of the archegonium is about five times its original length, the young fruit, which is a fusiform cellular body, does not occupy more than its upper half. In the meantime the cells forming the tissue subjacent to, or in the immediate neighbourhood of, the base of the fructified archegonium, have multiplied with such activity, that the end of the stem has again assumed the form of a cone, on the summit of which the fruit is borne, while the aborted archegonia are scattered round its sides. In its further development, the fruit grows much more rapidly in length than in breadth, and in consequence of its extension upwards being opposed by the resistant structure of the canal of the archegonium, its lower end presses downwards in such a manner as to cause the absorption, not only of the cellular tissue of the archegonium, which is subjacent to it, but of that of the conical summit of the stem. In

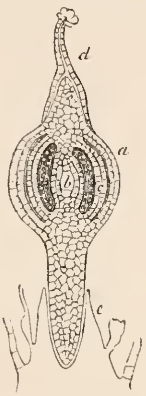
* From the very recent observations of Grönland (Mém. sur la Germination des Spores de quelques Hepatiques, Ann. des Sc. Nat. 3me. S. xx.), it appears that among the higher Hepaticæ with cut leaves, the first result of germination is always a branched and septate filamentous protonema, resembling that of the Mosses in its relation to the leafy stem.

† Hofmeister, *loc. cit.* pp. 65—71.; Bruch & Schimper, Bryologia Europæa, Fasc. i. p. 5.

this manner it becomes firmly implanted, the tissue which surrounds it assuming the form of a sheath, and receiving the name of vaginula. During this process, the dilated portion of the archegonium has increased in size, and has now attained about ten times its original length. Finally, it gives way at its line of junction with the vaginula, and is carried upwards on the summit of the still lengthening fruit.

77. *Development of the spores.* — The upper portion of the cylindrical fruit, which is destined to become the capsule, begins, some time after the calyptra has given way, to dilate rapidly. Soon after there is formed, by the separation of the external and superficial lay-

Fig. 166.



Section of half-ripe fruit of the same, 50 *diam.*

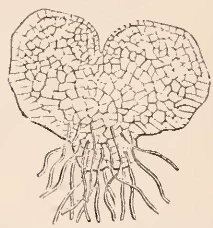
The globular dilatation exhibits the following parts: — *a*, the capsule. Within this, and separating it from the central portion, is a dark space, which corresponds to a cavity of the form of a hollow cylinder; *b*, columella; *c*, superficial layer of central portion; *d*, remains of archegonium; *e*, vaginula. (From fig. 164 to 166 from Hofmeister.)

ers of cells from the central portion, a cavity of the form of a hollow cylinder, the axis of which coincides with that of the fruit. At this stage, the central portion consists of an axile column of large cells, closely invested by a single layer of smaller ones (the columella); a superficial layer of cells, about four times as large as those last mentioned; and lastly, between the two, a layer of nucleated cells, with granular contents, the primary parent cells of the spores. The development of these last consists in the disappearance of the nucleus of each, and the substitution for it of two others; this being accompanied or followed by the division of the primordial membrane into two new vesicles, each of which encloses a nucleus. A cellulose membrane is now formed at the surface of contact of the two vesicles by which the original cavity is bisected. In the cavity of each of the resulting nucleated cells, two new ones make their appearance, apparently by contraction of the primordial membrane, either before or immediately after its division into two halves. On the surface of each half cellulose is secreted, so that the spherical cells which are thus formed possess a delicate cellulose external, and a very distinct inner membrane (primordial vesicle.) This last divides into four portions (the young spores), each of which becomes invested with a layer of cellulose. The ripe spore has been already described. The capsule now gives way at the line of its insertion on the pedicle which supports it. It is by the opening thus produced that the spores make their escape after the dislocation of the layers of cells immediately surrounding them. Phascum differs from all other genera in the absence of all trace of an operculum.

78. *Ferns.*—No two plants could be found which differ more completely from each other in the appearance which they present to the ordinary observer, than a Hepatica and a Fern, at the moment that the spores of each arrive at maturity; yet, in the history of their organisation and development a very close correspondence exists. The immediate result of the germination of the spore of a Fern is a frond similar to that of the simpler forms of Hepatica; on this frond antheridia and archegonia are formed. In each fructified archegonium, a central germ-cell is developed to a new individual, widely different in organisation from the parent. It, in its turn, produces spores, the germination of each of which is the commencement of a new circle of phenomena similar to the one which precedes it. Dividing this circle into two periods, as before, we have the following stages in the development.

79. *First period.** —*Germination of the spore.* — The mature fern-spore consists of a delicate transparent vesicle, which is invested in a brown resistant external membrane. Germination consists in the budding out of the transparent vesicle so as to form a nipple-shaped projection, which penetrates the external membrane. The projecting part divides repeatedly by transverse septa. About the same time a second budding out takes place in the opposite direction, which is destined to the formation of a root. By the further growth of new cells, a flattened two-lobed organ is formed — the Prothallium.

Fig. 167.



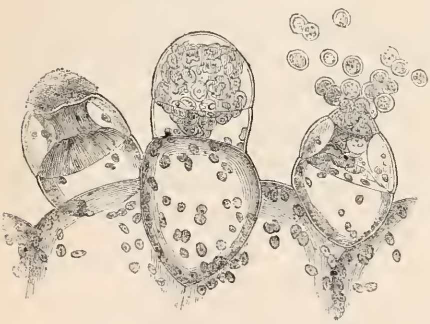
Early condition of prothallium of Gymnogramma chrysophylla, about 20 *diam.* (Henfrey.)

80. *The antheridia.*—The antheridia are situate on the under surface of the prothallium,

* Hofmeister, *l. c.* pp. 78—82.

and take their origin as follows. A hemispherical projecting portion of one of the superficial cells is cut off from the rest by a horizontal septum as in Anthoceros. This is divided by a single transverse septum. In the resulting terminal cell a second septum is formed, inclined to the horizon at a small angle, which is followed by a third, inclined in the opposite direction. Both of the cells resulting from these divisions, and subjacent to the last-formed septa, are again divided by perpendicular septa coinciding with the axis of the papilliform rudiment. In one of the resulting cells there is then formed a perpendicular septum, which meets its predecessor at an angle of 45.° Hence results a club-shaped body, consisting of a four-sided central cell, filled with granular mucus, and enclosed by six others, having the following arrangement. Four of the form of segments of a hollow cylinder, which are in contact by their edges, surround the central cell on all sides. It is surmounted by a fifth, which is hemispherical (the terminal cell last formed). A sixth, the cell resulting from the first division by a horizontal septum, is cylindrical, and serves as a pedicle on which the whole is supported. The central cell is converted by a successive division into a round group of dice-shaped cellules, in the interior of each of which a delicate lenticular vesicle is formed, which contains, rolled up in its interior, a spiral filament. The ripe antheridium bursts at its summit, and the escape of its contents is, as in the preceding cases, followed by the bursting of the vesicles, and the commencement of the active motions of the spiral

Fig. 168.



Antheridia of Pteris aquilina, 260 *diam.*

On the right is seen an antheridium from which cells containing antherozoids are escaping; in the centre another, which has not yet burst; on the left a third, which has already discharged its contents. (Thuret).

filaments (antherozoids.) In each filament the extremity which is directed forwards during motion, is broader than any other part, while the opposite extremity (posterior) tapers off into a long filament. The anterior coil of the spiral bears on the surface furthest from its axis a number of delicate cilia. The motion of the antherozoid is of two kinds—of progression and of revolution round the axis of the spiral.

81. *The archegonia.* — At a period somewhat later than that at which the rudiments of the antheridia begin to appear, there commences on the inferior aspect of the prothallium, and in the immediate neighbourhood of the notch by which its anterior margin is bisected so as to form two lobes, an active development of new cells. The result of this is the formation of a cushion-like projection of the surface bordering the notch above mentioned, upon the anterior aspect of which the archegonia are formed.

82. Each archegonium takes its origin from a cell, which is distinguished from those surrounding it by the comparative abundance of granular mucus which it contains, and by the presence of a distinct central vesicular nucleus. This cell divides by a horizontal septum into a superior and an inferior portion. It is from the latter, which is hemispherical, that the papilla which forms the rudiment of the projecting portion of the organs is formed. It consists, as in the Hepaticæ and Mosses, of four contiguous columns of cells, each of which is a half segment of a cylinder, the whole being surmounted by a hemispherical terminal cell. In the further development, varieties are often observed, even on the same prothallium. This is dependent on the mode in which the canal occupying the axis of the mature archegonium is produced. Most frequently a central column of cells is formed in exactly the same manner as an Anthoceros. The cells forming it are afterwards absorbed and disappear, leaving a four-sided canal. In the other case, the canal results simply from the separation of the four piles of cells along their common line of contact. This is the arrange-

Fig. 169.

Archegonium of Asplenium septentrionale, 250 *diam.*

a, germ-cell enclosed in its parent-cell; the membrane of the latter is still perfect, and separates its cavity from *b*, the axial canal. (Hofmeister.)

ment which occurs constantly among the Equisetaceæ, Lycopodiaceæ, and Rhizocarpeæ. In reference to the mode of origin of the germ-cell, there is some difference of opinion. According to Hofmeister,* the cell which contains it originates by the formation of a tangental septum in the lowest of the cells, constituting one of the four columns of

* *Loc. cit.* p. 80.

which the rudiment is composed. According to Mr. Henfrey*, on the other hand, the germ-cell is contained in the superior, and consequently deeper, of the two portions into which the primary nucleated parent cell of the organ divides by a horizontal septum; and is distinguishable before the formation of the papilla-like structure has commenced. This account of the matter is not only supported by analogy, but, as it appears to us, in a very marked manner by Hofmeister's own drawings.

83. *The embryo.*—Immediately after the entrance of the spiral filaments into the cavity of the archegonium, the cells which immediately surround it multiply rapidly, in consequence of which the cushion-like projection of the inferior surface of the prothallium increases in size. At the same time the germ-cell is transformed into an irregularly egg-shaped body, which consists of minute cellules, and may be considered as the primary axis of the future fern. It originates in the same manner as the rudiment of the fruit of the Mosses and Hepaticæ, and elongates by repeated divisions of a terminal cell by septa, inclined alternately in opposite directions. It consequently presents but one growing point, which is directed, not towards the orifice of the archegonium, but, on the contrary, towards the centre of the cushion-like mass, by the cells of which it is surrounded. Soon after, however, there appears on the side of the egg-shaped embryo, which is directed towards the notch in the anterior margin of the prothallium, a second growing projection of its surface. This projection, at first conical, becomes, as it enlarges, compressed from above downwards. No sooner is this the case, than it bursts through the superficial cellular layer of the prothallium, at a point which is invariably a little anterior to the base of the archegonium—between it and the angle of the notch. It now assumes the form of a symmetrical leaf-like organ, and begins to project beyond the notch of the prothallium. The further development consists in the appearance in the axil of this primordial leaf, of a new axis, the permanent stem of the young plant. From this axis all the succeeding leaves take their origin, each diverging from its immediate predecessor at an angle of 60°.

84. *Sporangia and spores.*—At a point of the surface of the frond, which always corresponds to the termination of a vascular bundle, a lacuna is formed under the epidermal layer, by the separation of that structure from the subjacent tissue. The floor of this cavity consists of a pavement of tessellar cells, some of which grow out into nipple-shaped projections. In each of these, the projecting portion is separated from the rest by a horizontal septum, which is soon followed by several others superior and parallel to it. The last-formed terminal cell now enlarges, and assumes a globular form, and is converted by a process similar to that to be described below in the rudimentary sporangium of Equisetum, into a central mass of nucleated cells, with grumous contents (parent cells), enclosed in a capsule formed of a single layer of others, which are tabular. In each parent cell, the central nucleus afterwards disappears, and is replaced by four others. This is followed by the division of the primordial sac into four portions, around each of which a cellulose membrane is formed. This membrane becomes the epispore; a second (endospore), which is distinguished by its greater delicacy, being subsequently formed within it.*

85. *Equisetaceæ.*—The history of the development of the Equisetaceæ corresponds in most respects with that of the Ferns.

86. *First period.*†—*Germination of the spore.* — The spore of Equisetum consists, in its ripe condition, of a delicate, colourless internal vesicle, which is surrounded by a more or less resistant granular membrane, and contains a central nucleus, and a yellowish grumous fluid, in which swim oil and chlorophylle granules. The first change observed in germination consists in the division of the nucleus into two, and the subsequent formation of a septum between the two corresponding halves of the spore-cell. Of these halves, the larger contains nearly all the chlorophylle, and is developed to the stem; the smaller, the contents of which are almost colourless, is the commencement of the root. The prothallium, which results from repeated cell-division of the larger half, is an irregularly riband-shaped expansion, growing and branching repeatedly at the extremity furthest from its point of origin, and consisting of large, delicate-walled cells, containing much chlorophylle. One of the branches is usually observed to be larger than the rest, and it is upon it that the reproductive organs are formed.

87. *Antheridium.*—The rudimentary antheridium of Equisetum consists, like that of preceding families, of a papilla, composed of four conjoined vertical piles of cells, each pair slightly overlapping the pair preceding it. In each of the cells constituting this rudiment a tangential wall is formed, dividing it into an inner three-sided, and an outer tabular cell. The inner cells, which form a central oval mass, are soon observed to be filled with finely granular mucus; the tabular cells, on the contrary, contain chlorophylle, and form the wall of the future antheridium. The further development of the central mass corresponds entirely with what has been described in other families. The antherozoa are larger in Equisetum than in any other known example. They originate by the deposition of a gelatinous linear thickening, in the form of an imperfect ring, parallel to the plane surfaces of the discoid vesicles in which they are enclosed. When fully formed, they resemble, in almost

* On the Development of Ferns from their Spores' Trans. of Linnæan Society, vol. xxi. p. 135.

* Schacht, Entwick. des Sporangiums einiger Farrnkraeuter Bot. Zeitung, 1849. p. 537.

† Hofmeister, *l. c.* pp. 97—103.; Milde, Entwickelungsgeschichte der Equiseten, &c. Bonn, 1852.

every respect, those of the Ferns. The antheridia of the Equisetaceæ are placed, not upon

Fig. 170.

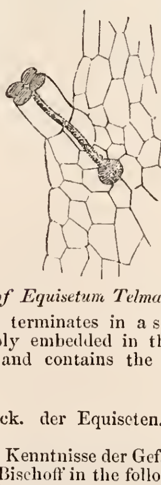
Antheridia of Equisetum, 300 *diam.*

a, ripe antheridium, from which the antherozoids are beginning to escape; *b*, unripe antheridium. (Hofmeister.)

the inferior surface, but along each margin of the principal branch of the prothallium.

88. *Archegonium.* — The archegonia were first discovered and figured by Milde* in Equisetum Telmateia, and have been since more completely described by Hofmeister† and Bischoff‡ in two other species. The projecting papilliform portion consists, according to the last-mentioned observer, of eight cells, of which the four lower, in apposition to each other, have the general form of truncated cones, each presenting two flattened surfaces by which it is united to its two neighbours. The upper, in the same relation to each other, are nearly cylindrical, but are slightly rounded at their summits. The axis of the organ is occupied by a quadrilateral intercellular passage. The whole is supported on a base, which consists of two or three rows of cells

Fig. 171.



Archegonium of Equisetum Telmateia, 200 *diam.*

The axial canal terminates in a spherical cavity, which is deeply embedded in the tissue of the prothallium, and contains the germ-cell. (Bischoff.)

* Zur Entwick. der Equiseten. Bot. Zeitung, St. 32, 1852.

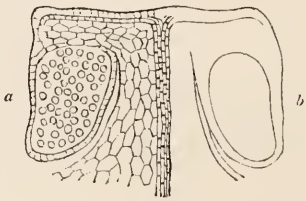
† Beiträge zur Kenntnisse der Gefässkryptogamen (referred to by Bischoff in the following paper.).

‡ Ann. des Sc. Nat. 3me S. t. xix. p. 234. (Extract from Bot. Zeitung, St. 6. Feb. 1853.).

superimposed upon each other, which combine to form a circular wall round a central cavity, which contains the germ, and is the termination of the quadrilateral canal. On the transformation of the germ-cell into the embryo, observations are as yet wanting.

89. *Spores and sporangia.*—The organs upon which the spore-cases are supported are arranged in whorls round the upper part of the fruit-bearing stem. They seem to be modifications of the ordinary stem-leaves, on which account they have received the name of *sporophylla*. In its earliest condition, the sporophyllum is a cellular projection of the surface; but, as it advances towards maturity, it assumes the form of a hexagonal disc

Fig. 172.

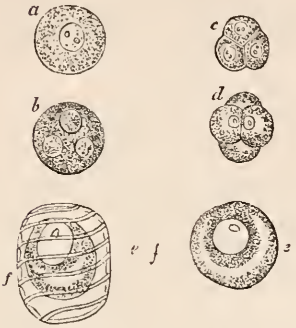


Vertical section of one of the sporophylla of Equisetum limosum, 100 *diam.*

a, mature sporangium; *b*, another in outline. The capsule of the sporangium is composed, when ripe, of the external layer of cells only, in consequence of the absorption of the two inner layers, which resemble in their structure those described more at length in the sporangium of Selaginella (§ 94.), and seem destined to afford the materials for the rapid growth and development of the mother cells of the spores.

attached by a pedicle at its centre. Upon the surface of the disc which faces the stem, the spore-cases are formed. Each spore-case originates as a little papilla, and consists of a large central cell, which is invested by a single layer of others of smaller size. As the organ enlarges, these last are transformed into a capsule consisting of three concentric layers, within which is enclosed a mass of cells exhibiting large central nuclei and grumous contents. In each of these cells the nucleus is afterwards replaced by two others similar to it, which almost fill the cavity. These, however, soon disappear, and now four globular nuclei, much smaller than their predecessors, present themselves, and are arranged, as in the Hepaticæ, towards the four angles of a regular tetrahedron. Around each nucleus a tetrahedral cell is formed, within which, after it has become detached from its fellows, there is deposited on the inner surface of its membrane, a gelatinous transparent layer. Within this layer, and immediately surrounding the nucleus, may be distinguished the primordial vesicle, on the surface of which the cellulose membrane of the future spore is secreted, as well as the two parallel, elastic fibres by which it is surrounded. When the spore is ripe, these last, which are external to the spore membrane, and consequently formed before it, line the inner surface of the parent

Fig. 173.



Development of parent cells of the spores of the same.

a, one of the nucleated cells which constitute the central mass of the young sporangium; *b*, the central nucleus has disappeared, and is replaced by four others, one of which is out of focus; *c*, the cell is divided by six septa into four somewhat tetrahedral compartments. This object has by mistake been represented relatively smaller than the rest; *d*, the four compartments (special parent cells of the spores), are about to separate from each other: *e*, mature special parent cell. In its interior we observe the nucleated spore, and between it and the membrane of the parent-cell, the coils of the two elastic fibres; *f*, the free spore; the spiral fibres, which remain for a short time after its escape from the parent-cell, attached by their middle points to its membrane, have disappeared.

cell, from which the gelatinous thickening has now disappeared. Soon after, springing asunder from each other, they tear the membrane of the parent cell, retaining, however, their central attachment to the surface of the spore.

90. *Lycopodiaceæ.**—The large spore (macrospore) of Selaginella, consists, when ripe, of an internal spherical vesicle of delicate structure (endospore), which is enclosed in a resistant epispore. The endospore contains a fluid, in which float mucous and oleaginous granules only, its nucleus having disappeared. On its surface are observed three linear projections, all of which converge towards one point, the summit of the spore. The epispore, a structure of later formation, is composed of two layers, the internal of which is distinguished from the other by its remarkable transparency. The external surface is scattered over with acuminated projections, which are connected with each other by a network of minute ridges.

91. The development of the prothallium commences (usually several months after the macrospore has been sown) by the deposition of several cells on the internal surface of the proper spore membrane, at a point subjacent to that towards which the three external ridges converge. Whether these cells are originally developed *in situ*, from a single parent, or existed before, lying free in the cavity of the spore, is uncertain. Hofmeister inclines to the latter opinion. At first the prothallium is a cellular expansion of circular form, which enlarges by growth at its periphery, and lines the upper part of the proper membrane of the spore. At its centre it is of considerable thickness, and is composed of several layers of cells. Towards its margin it becomes gradually thinner and thinner, its two surfaces at last converging at a very acute angle, so as to become continuous with those of the spore membrane.

* Hofmeister, *l. c.* pp. 118—124.

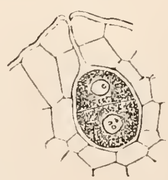
92. *Archegonia.*—The first-formed archegonium is always found to occupy the centre of the upper surface of the prothallium; its successors surrounding it at various distances. A superficial cell, distinguished from its neighbours by the quantity of granules which it contains, is divided into two by a transverse septum. From the upper of the resulting compartments is developed a papilliform projection, which is composed, as in the Equisetaceæ, of two double pairs of cylindrical cells, surrounding an axial intercellular canal. In

Fig. 174.

Section of unimpregnated archegonium of Selaginella denticulata, containing the granular germ-cell, 400 *diam.*

the lower is contained a vesicular nucleus, the germ-cell of the fully formed archegonium. Its cavity becomes continuous with the axial canal by the solution of its membrane.

Fig. 175.



Archegonium of the same immediately after impregnation, 600 *diam.*

The germ-cell has enlarged considerably, and divided by a transverse septum.

93. *The embryo.*—About the time that the formation of archegonia is completed on the upper surface of the prothallium, there is developed, on its inferior aspect, a tissue composed of cells much larger than any of those previously existing. This tissue projects, in the form of a cushion, into the cavity of the spore. In general one only of the many archegonia receives the necessary fructifying influence. In this the germ-cell divides repeatedly by transverse septa, as the result

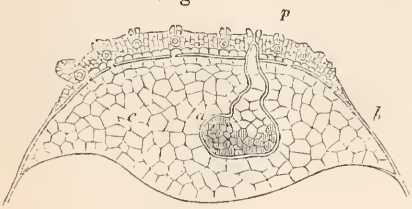
of which a structure is formed composed of a series of cylindrical cells placed end to end. The growing extremity of this body, the so-called *suspensor*, penetrates the single layer of cells which separate it from the inferior surface of the prothallium, and buries itself in the cushion-like mass. A new development now commences in the terminal cell, which is divided by a succession of septa inclined alternately in opposite directions.

Fig. 176.

Egg-shaped rudiment of embryo of the same attached to the suspensor, from the terminal cell of which it has originated, 300 *diam.*

From this results an egg-shaped body, the primary axis of the embryo, which, as it enlarges, causes the absorption of the cells by which it is immediately surrounded. Soon after a new (secondary) axis is developed,

Fig. 177.



Section of contents of upper part of macrospore of the same, 120 *diam.*

a, prothallium, continuous at its periphery with *b*, the original inner membrane of the spore; *c*, cellular body subjacent to prothallium, which projects into the cavity of the spore; *a*, commencement of secondary axis of growth of the embryo; below *p* are observed the remains of the archegonium within which the embryo originated. Several other unfructified archegonia are seen in section.

the direction of which (obliquely upward), is nearly opposite to that of its predecessor. It finally makes its escape from the cavity of the spore by penetrating the prothallium near its centre, bearing upon its summit the first pair of leaves of the young plant.

94. *Sporangia and spores.* — The sporangia of Selaginella denticulata are formed in the axils of the leaves of the fertile branch, in the following manner. A superficial cell of the stem, the position of which is always immediately above the middle of the line of insertion of the leaf, is developed to a nipple-shaped projection. The centre of this body is occupied by a large cell, which is enclosed by a single layer of others, and supported

Fig. 178.

Two germ plants of Selaginella Martensi, which have taken their origin from a single macrospore, 5 *diam.*

on a short pedicle. As it advances towards maturity, the spore-case consists of a capsule of three layers. Of these the external or epidermic, is composed of narrow prismatic cellules containing only a transparent fluid. The cells of the middle layer are tabular, and contain starch granules, while those most internal are narrow and somewhat columnar, with very delicate walls. Within this capsule is enclosed a central mass of larger cells, which exhibit central nuclei and granular contents. These, which are the parent cells of the spores, are at first intimately united, but afterwards lie loose in the cavity of the spore-case. Up to this point the development of all the sporangia is uniform. In those in which macrospores are to be produced (oophoridia), one of the parent cells, in no respect different from its fellows in structure, continues to increase in size while they disappear. Its nucleus is soon replaced by four others, which arrange themselves, as in Equisetum, towards the four angles of a regular tetrahedron. Septa are afterwards formed, which divide the cell into four compartments, in each of which a spore is developed. The spore at first exhibits only a delicate membrane, but as it approaches maturity the three converging ridges, and, finally, the external tegument, the structure of which has been already described, are formed upon its surface. No sooner is this process completed than the membrane of the parent cell disappears, the four spores retaining their relative position, however, to each other, apparently attached by the remainder of the septa. It is at the point at which the spores are in relation with the centre of the mother cells, that the three ridges converge, as well as the three lines by which the valves of the external tegument give way to allow of the growth of the prothallium.

95. In those sporangia in which microspores are to be formed, *all* of the original parent cells exhibit a development which corresponds with that which is above described as occurring in *one* only in the *oophoridium*, with this exception, that they do not attain the same dimensions. Hence results a large number of microspores which resemble the macrospores in the structure of their internal membrane, and external three-valved tegument, but differ

completely in their mode of germination. After lying a certain time on a damp surface, their inner cavities are found to be occupied by a number of small spherical cellules, each of which contains in its interior a spirally coiled fibre (antherozoid). By the dehiscence of the valves of the external tegument,

Fig. 179.

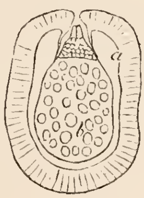
Valvate dehiscence of microspore of Selaginella helvetica, six months after sowing, showing escape of antherozoids, 300 *diam.*

the antherozoa are set free; and it is presumed, that it is by their agency that the archegonium is fructified, after the prothallium has been laid bare by the bursting of the macrospore at its apex.

96. *Rhizocarpeæ.*—In describing the mode of reproduction of the Rhizocarpeæ, we shall confine our attention to the genus Pilularia, respecting which the most exact researches have been made.

97. The macrospore of Pilularia is an egg-shaped body, presenting an equatorial constriction. It consists of an internal proper membrane (endospore), the so-called embryo sac,

Fig. 180.



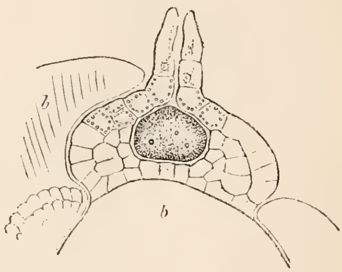
Section of macrospore of Pilularia some time after germination, 50 *diam.*

a, two layers of the exospore, the outer, vertically striated, the inner, homogeneous; *b*, cavity of endospore bounded superiorly by the prothallium, the papillæform summit of which projects through the canal of the exospore.

which is surrounded by a white coriaceous exospore. This last exhibits two distinct layers, of which the internal is colourless and vitreous, without trace of structure; while the external appears to be formed of prismatic columns fitting closely together, which are more distinct at the lower end of the spore, while they disappear entirely towards its smaller end or apex, at which point the exospore forms a papilliform projection open at its summit. From this arrangement there results a canal, which is immediately surrounded by the thickened and dentate margin of the vitreous layer, and leads to the apex of the endospore.

98. *The prothallium.*—The first indication of the commencement of the germination of the macrospore is the formation of a lenticular accumulation of granular plasma, at the summit of the endospore, which had previously contained only starchy, mucous, or oleaginous granules. Soon after there appears in the same position a delicate cell of similar form, the upper surface of which is in contact with the endosporal membrane, and is immediately subjacent to the aperture in the exospore. It is in all probability from this cell, although the earlier stages of the development have not been clearly made out, that the prothallium takes its origin. A day or two after germination it consists of a central cell, which is surrounded by a single layer of others of smaller dimensions. Four of these last are invariably found interposed between the upper surface of the large cell and the spore membrane; the septa by which they are separated being perpendicular, and at right angles to each other. Soon after the central cell itself divides by a transverse septum into two; of these the upper, of globular form, contains a large vesicular nucleus, the future germ-cell. The lower, which is tabular, divides repeatedly by vertical septa, so as to form a single layer of cells which intervenes between the cavity of the archegonium and that of the spore. In the meantime the four cells which surmount

Fig. 181.



Vertical section of prothallium of the same at the period of impregnation, which passes through the axial canal of the archegonium, and exposes

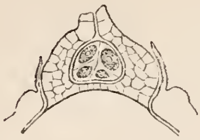
a, the germ-cell; *b*, cavity of macrospore; *b*, outer, and *c*, inner layer of exospore, the apicial canal of which (§ 97.), it completely occupies.

the germ-cell extend upwards in the form of four papillæ, separated from each other by an axial canal, which burst through the proper spore membrane, and finally project beyond the aperture of the exospore. By the absorption of the central cell, its cavity becomes continuous with that of the vertical quadrilateral canal above mentioned.

99. *The embryo.*—In consequence of the presumed entrance of the antherozoids into the cavity of the archegonium, the germ-cell enlarges, and is transformed by repeated division into an embryo, which is at first a somewhat meniscus-shaped body, formed of minute cellules. Soon after, a conical projection of its upper surface presents itself, which rapidly

increases by the repeated division of a terminal cell by alternately inclined septa. The

Fig. 182.

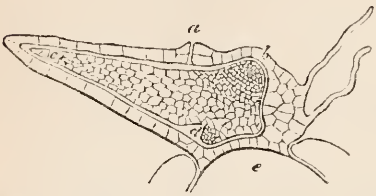


The same after impregnation, 150 *diam.*

The papilla has been broken off in making the preparation.

direction of growth of this structure, which is the first leaf of the embryo, is obliquely upwards. In its axil is formed the primary axis,

Fig. 183.



Embryo of Pilularia globulifera, 10 *diam. The embryo is still enclosed in the prothallium, the tissue of which has expanded so as to form an investment for it.*

a, remains of papilla of archegonium with its canal; *b*, first root; *c*, first leaf; *d*, primary axis; *e*, cavity of macrospore.

and soon after, as a lateral development from this last, the second leaf. In the meantime the first root makes its appearance as a rounded projection, which grows from the upper surface of the embryo, in a direction opposite to that of the first leaf. Both of the last-mentioned organs finally burst through the remains of the prothallium, and become free.

100. *Sporangia and spores.*—The organ in which the sporangia of Pilularia are contained is an egg-shaped body, supported on a short, curved pedicle, which springs directly from the creeping stem, in the axil of one of the awl-shaped leaves. It presents a tough, coriaceous, cellular coat, which encloses a cavity, which is divided into four compartments by vertical septa, and subsequently dehisces in four valves. The middle of the internal surface of each valve is, from the first, marked by a ridge of gelatinous cellular tissue, from which the sporangia take their origin as a vertical series of projections. Their development remains up to a certain time the same, whether they are to produce large or small spores. All are found to exhibit at this period a central mass of cells, containing nuclei and grumous fluid, which is surrounded by a double capsular layer. In each of the central cells, the nucleus soon after is replaced by four others of smaller size, around which are formed four tetrahedral secondary cells, which are the immediate parents of the spores. In the lowest of the vertical series of sporangia which corresponds to each valve, one only of the original central cells continues its development, the rest becoming abortive, and finally disappearing. The four spores, which are formed just as in Selaginella, at length become free by the absorption of the cell in which they are enclosed, and for a time continue to enlarge equally, while their walls are thickened by internal gelatinous deposition. Soon, however, one begins to exceed the rest in growth, and finally occupies the whole cavity of the sporangium, which is subsequently burst by the swelling of the exospore, which is produced when it is subjected to the influence of moisture.

101. The microspores are developed precisely as in Selaginella. The exosporal membrane

Fig. 184.

Microspore of the same, 600 *diam.*

The inner membrane projects through the outer, which has given way. A few of the cellules containing spermatozoids have escaped.

dehisces in three valves, the proper membrane of the spore at the same time giving way irregularly, to allow the escape of numerous little globular cellules. These cellules contain, in addition to starchy and mucous granules, parietal lenticular vesicles, each of which encloses a delicate, spirally coiled antherozoid, which moves actively in water.

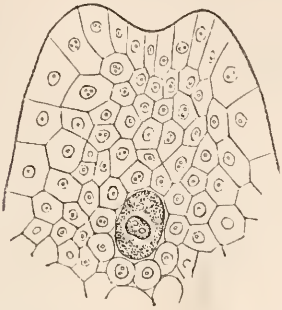
102. *Phanerogamia.*—Between the higher vascular Cryptogamia, and the simplest forms of flowering plants, there exists, as has been already noticed, a wide chasm of obscurity. The researches, however, of Hofmeister, have shown that in the Coniferæ the embryo is formed upon a plan which presents the most striking analogies to what is observed among the Rhizocarpeæ and Lycopodiaceæ; and that, in fact, their development stands intermediate between that of the plants just mentioned and the angiospermous Phanerogamia.

103. *Phanerogamia gymnospermia.*—Following the same plan of description that we have adopted in the previous section, we shall confine our attention to the Abietineæ, of the development of which Hofmeister has furnished us with a most complete account. The so-called ovule consists, at the time of the scattering of the pollen, of a short and thick nucleus of delicate cellular tissue, which is enclosed in a single, somewhat fleshy integument, leaving open a wide micropyle canal.* In the centre

* For the origin and signification of botanical terms in common use we refer the reader to any of the elementary works on Botany.

of the nucleus there exists an ovoidal embryo-sac, which owes it origin to the coalescence of a vertical and axial series of cells. At this period it contains only granules of starch and

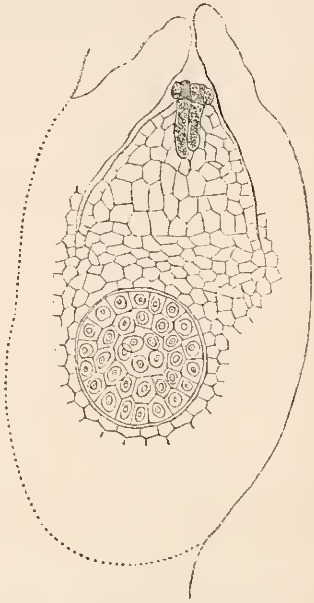
Fig. 185.



Section of nucleus of ovule of Pinus Austriaca, in the centre of which is observed the young embryo-sac, 150 *diam.*

mucus, the nucleus which it at first contained having disappeared. It corresponds, as will be seen as we proceed, to the internal membrane of the ripe macrospore of the Rhizocarpeæ and Lycopodiaceæ. The pollen grain in the Coniferæ generally itself reaches the summit of the nucleus by means of the wide micropyle. From each grain emanates a tube, which penetrates for a short distance into the tissue of the nucleus; not, however, until it has remained for some time upon its summit. In the meantime numerous free nuclei have become visible in the embryo-sac, which immediately afterwards "presents itself filled with a large number of radially elongated cells, which are arranged in a concentric layer." These continue to multiply by septa in all three directions, until the beginning of winter, at which period the wall of the embryo-sac is so delicate as to be indistinguishable. During the winter months these cells undergo no further change, except that their walls are thickened by internal gelatinous deposition. In the beginning of March of the second year, both the gelatinous material and the cell-wall disappear, the primordial sacs lying free in the cavity of the embryo-sac, each containing a large globular nucleus. Shortly after, the nucleus of each cell disappears, and is replaced by two or four smaller ones, round each of which new spherical secondary cells are formed. The parent cell is dissolved, and immediately after, the same process is repeated in the secondary cells. While this is taking place, the embryo-sac has increased to twenty times its former volume; its membrane has become resistant and vitreous, while throughout the whole ovule, with the exception of its summit, an active cell growth has taken place. Towards the middle of May the permanent cellular body which afterwards fills the whole embryo-sac, originates by the application, in successive layers, of the cells contained previously in its cavity, to its membrane. By the continuation of this process, the sac becomes a second time filled with cellular tissue.* Two or three of the cells subjacent to the micropyle end of the embryo-

Fig. 186.



Section of naked ovule of Pinus maritima, as observed in January of the second year, 150 *diam.*

The spherical embryo-sac is filled with cells, the walls of which are already thickened by gelatinous deposition. Two pollen grains occupy the funnel-shaped space between the wide micropyle and the summit of the nucleus. The cellular tissue of the latter is penetrated by two tubes emanating from the pollen grains. At the dotted line the tissue of the ovule becomes continuous with that of the spermophore.

sac now become larger than the rest, and are destined to contain the germs of the future embryos. As their development proceeds, these bodies, the so-called corpuscula, assume an elongated, oval form, and the space intervening between their summits and the membrane of the embryo-sac is occupied by four small cells on the same level, which are

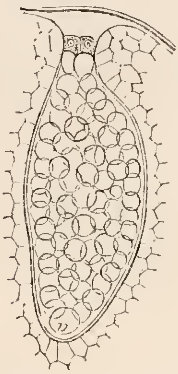
Fig. 187.

Four cells which surmount the corpusculum of Pinus sylvestris, seen from above, 200 *diam.*

* To this tissue is commonly applied the term "albuminous body." It corresponds in its mode of origin with the "endosperm" (§ 106.) of other Phanerogamia.

separated from each other by as many vertical septa, meeting at right angles. Each corpusculum is likewise surrounded on all sides by a single layer of cellules resembling pavement epithelium, and exhibits in its interior a nucleus which is usually placed at its superior extremity. After some time the nucleus disappears, and now a number of transparent vesicles become visible, which accumulate for the most part towards the extremities of the corpusculum.

Fig. 188.

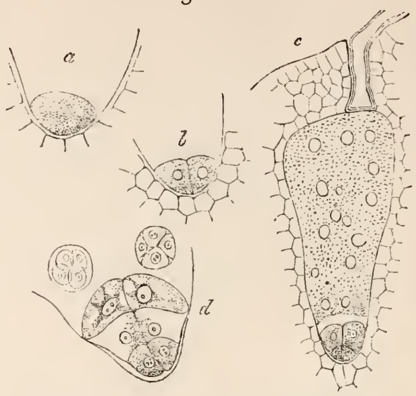


Corpusculum of the same in section, immediately before impregnation, 200 *diam.*

Its cavity is filled with transparent vesicles, and bounded superiorly by four granular cells, the position and relations of which recal very forcibly the arrangement which presents itself in the rudimentary archegonium among the higher Cryptogamia.

104. The growth of the pollen tube, which has been for many months arrested, at last recommences ; the membrane of the summit of the embryo-sac at the same time becomes attenuated, and immediately after is penetrated by the narrowed end of the pollen tube, which is brought into immediate contact with the summit of the corpusculum, the four cells which previously surmounted it having disappeared. At this time, the corpusculum exhibits in its interior, at the end opposite the pollen tube, a single vesicle, much larger than those by which it is surrounded, within which is afterwards developed a secondary cell, occupying more than half its cavity. This cell, which is convex above, is applied by a flattened inferior surface against the wall of the corpusculum. It soon divides by a longitudinal septum into two, each of which is nucleated. These two cells, which occur throughout the Coniferae, form the commencement of the suspensor. They next divide by a second pair of vertical septa, at right angles to the first ; and in each of the four cells which result, a succession of horizontal septa are formed, by which they are converted into four vertical columns intimately united to each other. The suspensor lengthens in one direction only, partly by the repeated division of the four inferior terminal cells, partly by the interstitial growth of those first formed. Soon it bursts through the

Fig. 189.



Corpusculum of the same, 120 *diam.*

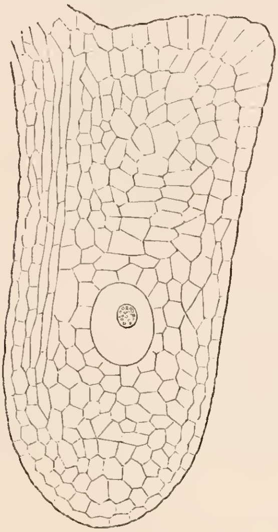
The four cells by which it is bounded superiorly have disappeared. The pollen tube is still in contact, by its flattened extremity with the corpusculum, and by the rest of its surface with the cells of the albuminous body. *a*, 300 diam. Earlier stage of development of lower end of the same. A single germ-cell is applied to its wall. *b*, 300 diam. Division of germ-cell into four by two vertical septa, of which one only can be seen on section. *c* and *d*, 250 diam. Division of the four resulting cells by a succession of transverse septa. Above *d* are two of the numerous complexes of cells, which at this time float in numbers in the corpusculum. (From fig. 172 to 189 inclusive, are after Hofmeister).

membrane of the corpusculum at its lower end, and becomes immersed in the tissue which occupies the embryo sac, the cells of which, at the same time, become less intimately united than before. The four series of cells of which the suspensor is formed, now separate, and, from the terminal cell of each, the rudiment of an embryo takes its origin. Its development commences, like that of the embryos of the Hepaticæ and of the first leaves of the Ferns and Equisetaceæ, by the repeated formation of alternately inclined septa in a terminal cell ; these being followed by vertical septa radiating from the axis, and, subsequently by others parallel to the external surface. Of the four embryos thus formed, one only advances to vigorous maturity.

105. *Phanerogamia angiospermia.*—The observations on record relating to the origin and development of the embryo among these plants are now so numerous, that although the conditions are much more complicated, and the difficulties in themselves much greater, we are, notwithstanding, more competent to draw our conclusions with confidence than we have found ourselves to be in our previous study of the Cryptogamia. Among the many examples at our disposal, we select two of the simplest, between which, at the same time, great differences present themselves in those respects in which the development is variable.

106. *Hippuris vulgaris.**—The already anatropous ovule of this plant consists of a cylindrical nucleus of delicate cellular tissue, along one side of which is observed a longitudinal fleshy ridge, terminating above in a short funiculus, by which the ovule is suspended from the apex of the one-celled ovary. One of the central cells of this nucleus becomes larger

Fig. 190.

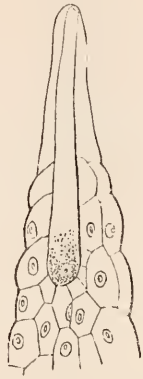


Section of naked nucleus of Hippuris vulgaris at an early stage, about 150 diam.

The embryo-sac is seen as a large central nucleated cell. (Unger.)

than the rest, from which it is further distinguished by its containing a free vesicular nucleolated cell-nucleus and granular fluid. This cell, the embryo sac, rapidly enlarges, and at the same time assumes an elongated oval form. A number of vesicles of various size are developed at the same time, at its micropyle extremity, all of which disappear some time before the scattering of the pollen. Shortly after this has taken place several new cells are formed, one of which, situated towards the upper end of the sac, begins at once to lengthen, and is finally converted into a tube closed at both extremities (germ-cell). The rest arrange themselves in vertical series, so as to form a continuous tissue (the endosperm), which completely occupies the lower part of the sac. *After* this, in consequence, as may be presumed, of the contact of the pollen tube with the membrane of the sac, the germ-cell is divided by a transverse septum into a tubular superior, and a spheroidal and much smaller inferior compartment. The

Fig. 191.

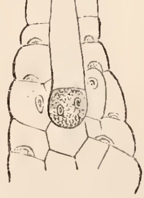


Upper end of embryo-sac of the same as observed immediately before impregnation, 250 diam.

The tubular germ-cell, the lower end of which is embedded in the nucleated cells of the endosperm, occupies its axis.

latter, which is the parent cell of the embryo, is divided by a vertical septum into two hemispheres. In these two new septa are formed, also vertical, but at right angles to

Fig. 192.



The same immediatety after impregnation.

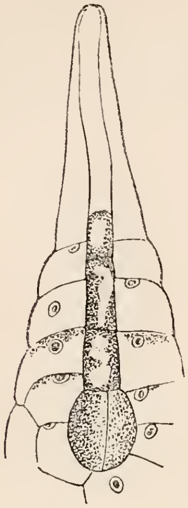
The germ-cell is now divided by a transverse septum into two compartments, the inferior of which is the parent-cell of the embryo. 250 diam.

the last. In the meantime, several new vesicles make their appearance in the upper tubular compartment of the germ-cell, which eventually become cylindrical, and arrange themselves, end to end, in its interior. The four cells of the embryo now divide by horizontal septa, which are succeeded by others parallel to its surface, and meeting their predecessors at angles of 45°. The globular body which is thus formed, consists of six-

* Unger, Botanische Beobachtungen, Entwick. des Embryos von Hippuris vulgaris. Bot. Zeitung, 1849, p. 329. Sanderson, On the Embryogeny of Hippuris vulgaris. Trans. of Bot. Soc. of Edinburgh, Feb. 1850.

teen cells, of which eight are superficial, and the other eight enclosed as a central spheri-

Fig. 193.

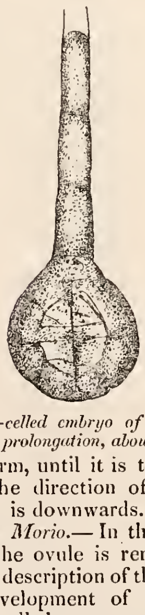


Later stage. Division of parent-cell of embryo by a vertical septum.

The vesicles contained in the upper tubular portion of the germ-cell have now arranged themselves so as to form a filamentous prolongation to the embryo, about 200 diam.

cal mass. By the frequent repetition of the same process it increases in size, still retaining

Fig 194.

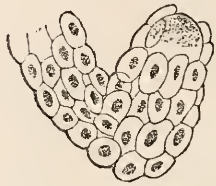


Isolated sixteen-celled embryo of the same, with its filamentous prolongation, about 150 *diam.*

its globular form, until it is transformed into an embryo, the direction of growth of the axis of which is downwards.

107, *Orchis Morio.*— In the Orchideæ the structure of the ovule is remarkably simple. The following description of the mode of origin and early development of the embryo, in Orchis Morio, all the stages of which we have ourselves followed, is taken from Mr. Henfrey's paper on Vegetable Reproduction, in the Annals of Natural History: — "The ovule springs from the placental surface as a single projecting cell, which, by subdivision, soon becomes a cellular papilla (the nucleus), composed of a central cell (the embryo-sac), surrounded by a simple cellular layer. The two coats gradually grow up over this, and by the greater elongation of one side the ovule becomes anatropous. The nucleus meanwhile loses its cellular coat, apparently by absorption, and appears as a large oval sac enclosed in the coats, consisting in fact merely

Fig. 195.



Early condition of ovule of Orchis mascula.

The embryo-sac is exposed in consequence of the absorption of the cells which previously surrounded it, 180 diam.

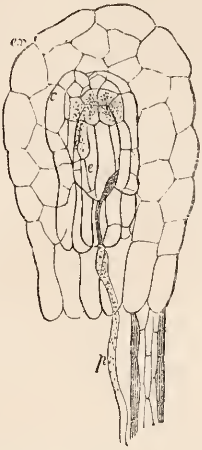
of an embryo sac. In the apex of this, about the epoch when the pollen falls upon the stigma, three cellules (embryonal vesicles), make their appearance at the upper end of

Fig. 196.

Isolated embryo-sac of the same immediately before impregnation, containing three embryonal vesicles, 180 *diam.*

the embryo sac, formed apparently by free cell-formation around a globule of protoplasm. The pollen masses on the stigma send down pollen tubes, which traverse the conducting tissue of the style, and make their way to the placentas, where they enter, ordinarily, singly (sometimes more than one) into the micropyle canals of the ovules, and come in contact with the outside of the apex of the embryo sac, immediately above where the embryonal vesicles lie; but the pollen tube does not penetrate the embryo sac. Soon after the pollen tube has reached the embryo sac, one (very rarely two) of the embryonal vesicles begins to swell, becomes divided by a cross septum into two cells, and while the upper one grows out in a filamentous form through the micropyle, by a continued process of cell-division, the lower cell enlarges, and divides repeatedly so as to form a cellular globule—the embryo, which in this plant does not go on to produce a cotyledon and radicle, as in most other cases. The filamentous prolongation, the use of which is not evident, but which seems analogous to the suspensor, presently to be mentioned, meanwhile decays away."*

Fig. 197.

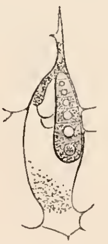


Ovule of the same at the period of impregnation.

x, the external integument; *c*, the internal, which immediately surrounds *e*, the embryo-sac. The pollen tube *p*, after passing the wide exostome becomes sensibly narrowed as it penetrates the canal leading to the embryo-sac, with the outside of which its termination is in contact. 180 diam.

108. *The anther and the pollen cell.*—The history of the development of the anther is remarkably uniform among the different families

Fig. 198.

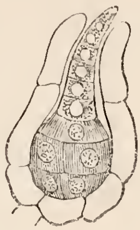


The same, some time after impregnation.

The remains of the pollen tube are observed to be still adherent to the sac. The rudiment of the embryo exhibits itself as a somewhat pear-shaped cell, divided towards its upper part by a succession of transverse septa, into numerous compartments. The lowest of these, larger and more granular than the rest, is the parent-cell of the embryo. 180 diam. (The above, from 191 to 198 inclusive, are original.)

of Phanerogamia. It at first appears in the young flower-bud as a cellular papilla, which grows out laterally from the floral axis. By continuous cell multiplication an organ is formed, in which may be distinguished a

Fig. 199.



Further developed embryo. (*Orchis Morio.*)

The embryo-sac is no longer distinguishable. The spheroidal embryo which completely occupies the cavity of the ovule is surmounted by a filamentous prolongation, which projects through the micropyle. 150 diam. (Henfrey.)

central cylindrical column (connective), along the antero-lateral aspects of which are attached two larger cellular masses; the outer surface of each is marked by a vertical furrow, indicating its division into two halves, which are the rudiments of the future *loculi*. In each half a single axile vertical column of cells soon becomes distinguished from those surrounding them by their greater size and granular contents. In each of these cells the nucleus disappears, and is replaced by two others, this being followed by a division of the cell contents (primordial membrane), which results in the formation of a new cell round each nucleus. By the repetition of this process a mass of cells — the parent-cells of the spores—is formed, which occupies the centre of each rudimentary loculus. The next change observed is the thickening of the walls of the parent-cells by gelatinous deposition on the interior surfaces. This is followed in all of them by disappearance of the nucleus, and consequent division of the contents of the cell (primordial membrane) into two portions, each surrounding a new nucleus. These, however, are only transitory formations, and are soon succeeded by four permanent nuclei, which are placed towards the four angles of a regular tetrahedron, each invested with a primordial sac containing a granular mucus, on the surface of which is soon secreted a gelatinous layer. In this manner the parent cell is divided into four compartments — the so-called special parent cells of the pollen grains. Within each compartment is now formed a new cellulose membrane on the surface of the primordial utricle. This is transformed into a resistant and coloured tegument, which is the outer membrane of the pollen grain, and exhibits various projections of its surface, which differ according to the species.

109. While these changes are taking place in the central mass of each loculus, the tissue forming its wall is transformed into a capsule of three distinct cellular layers. The inner

* Henfrey, On the Reproduction of the higher Cryptogamia, and the Phanerogamia. Annals of Nat. Hist., June, 1852.

layer consists of radiating prismatic cells, and is soon absorbed. The cells of the second layer are distinguished by their containing at first numerous starch granules, and afterwards by the deposition of spiral fibres on the inner surfaces of their walls. These are usually dice-shaped cells arranged in concentric layers. The external or epidermic layer consists of tabular cells in contact by their edges.*

110. *Review of the analogies which present themselves in the history of the development of the reproductive organs of the higher Cryptogamia and of the Phanerogamia.*—The families in question are distinguished by the presence of what is called "sexual reproduction" from all others. It is true that among the Characeæ, Conjugatæ, Vaucheriaceæ, and Desmideæ, the concurrence of two dissimilar parts is necessary for the development of the germ; but in them the phenomena do not present themselves in such strict conformity to law, and the anatomical relations of the germ to the organ which contains it are not nearly so complicated as in the plants under our consideration. Taking the sexual germ as our starting point, in comparing the history of the development of the phanerogamous with that of the cryptogamous plant, the following analogies present themselves:—

111.—1. *Analogies existing between the ovule, the anther, and the sporangium* — In Zostera marina the termination of a stem destined to bear reproductive organs, is broadened out in the form of a spatula, concave on one side, convex on the other. On the concave surface are observed, early in the development, two vertical series of papillæ—one on each side of the middle line—which are the rudiments of the organs which support the ovules and anthers. In each series, the two kinds of rudiments are arranged alternately in such a manner, that an ovule in one series is always on the same level with an anther in the other. The rudimentary organ which is destined to contain the ovule, commences as an imperfect ring of cellular tissue, on the inside of which is seen a little round projection—a bud in the axil of a leaf. From this projection is developed the ovule, with its tegments, just as described in Orchis Morio. The axis of its nucleus is occupied by a vertical series of cells. Of these the uppermost enlarges, and becomes detached from its neighbours, so as to form the embryo-sac.† If we compare this process with what occurs in Selaginella, we find in each case, a cell belonging to the stem in the axil of a modified leaf, which transforms itself into an axial organ. In each case one of the central cells enlarges and becomes detached—in Selaginella, to form the mother cell of four spores—in the phanerogamous plant, to become the embryo-sac.

112. The exact correspondence, step for step, which exists between the development of the anther, and that of the sporangium, will be best seen by successively comparing the descriptions contained in § 89 and § 108. It is rendered still more striking when we consider the very remarkable variations which present themselves in the structure of the anther among the Phanerogamia themselves; as *e. g.* in Zostera, among the Orchidaceæ, and other examples for the description of which space is wanting. The contemplation of these analogies leads us to remark how little relation there seems to be as respects the organs under consideration between the morphological import of the rudiment and its development. The ovule of Zostera is an axial organ, originating in the axil of a modified leaf; its analogue in development, the anther, is itself a bilateral foliar organ. The sporangium of Equisetum seems to originate as a leaf,—that of Selaginella, as an axis in the axil of a leaf.

113.—2. *Analogy between the embryo-sac, the pollen cell, and the parent cell of four spores* — In approaching this, the most difficult part of our inquiry, we must refer to the Coniferæ, as holding in so many respects an intermediate position. Of those stages of the development which *precede the act of impregnation* in Selaginella, the first, namely, the division of the parent cell into four compartments, and the formation of a spore in each, is entirely wanting in the Coniferæ. The prothallium—understanding by the term the organ of which the archegonia form a part—is represented by the corpuscula, between which and the archegonia, the resemblance in structure is very striking.—The difference in the mode of origin of the germ-cell, on the other hand, is no less remarkable. "Among the Cryptogamia there is," says Hofmeister, "only one germ-cell which completely fills the central cell of the archegonium, while in the Coniferæ, very numerous germ-cells swim in the central cell of the corpusculum, of which one only, applied against its lower end, is fecundated." In the gymnospermous Phanerogamia, all the steps of development which intervene between the parent cell and the germ, disappear; the latter originating altogether independently at the upper end of the embryo-sac. As the transformation of the germ-cell is the most important element in the process of development, it presents the greatest degree of constancy. It always commences by the formation of one or more septa, the direction of which, in relation to that of the first axis of growth, is transverse or nearly so.

114. In the Hepaticæ and Mosses one septum is formed, the inferior of the two resulting cells undergoing no further development, while the superior is transformed into the primary axis of the fruit. This fruit-axis, the apex of which is converted into a sporangium, is normally a leafless one. In the Mosses, how-

* Nägeli, Zur Entwick. des Pollens, &c. Zürich, 1842; Wimmel, Zur Entwick. des Pollens, &c. Bot. Zeit. 1850, S. 225.

† Hofmeister, Entwick. der Zostera. Bot. Zeit. 1851; Grönland, Beitrag. zur Kennt. der Zostera marina, &c. Bot. Zeitung, St. 10. 1851.

ever, examples frequently occur, in which its development is changed, under the influence of peculiar external circumstances, in such a manner that, instead of producing a sporangium it lengthens considerably, and bears symmetrically arranged leaves. Such a condition makes it more easy to compare the fruit of the Mosses and the leafy stems of the higher plants. In the Ferns and Equisetaceæ, again, only one transverse septum is formed; but here, it is the inferior secondary cell which is developed to the embryo, the direction of the first axis of growth being opposite to that of the archegonium. In Selaginella, a succession of transverse septa are formed, whence results a conferva-like filament, which lengthens downwards by repeated division of a terminal cell. At length the youngest cell is transformed into an embryo. Among the Coniferæ, the same process presents itself, with this important difference, that before it commences, the germ divides by two crucial vertical septa into four cells, which correspond to the four embryos which are afterwards formed. In all the Phanerogamia, probably without exception, the germ-cell divides, in the first instance, by a transverse septum into two cells, of which the upper is the larger. In some cases the lower cell is developed directly to a spherical cellular mass (as in Hippuris and Orchis Morio). Much more frequently, however, it is transformed into a conferva-like filament (suspensor) which lengthens by repeated division of an inferior terminal cell. At length the youngest cell, instead of lengthening, becomes spherical, and gives rise to the embryo by a process similar to that described above in Hippuris.

115. The organ to which the name suspensor is applied by Mr. Henfrey in Orchis Morio, differs materially from that of Selaginella, the Coniferæ, or from that described in the preceding paragraph. Its formation does not, like that of the true suspensor, precede, but follows the origin of the embryo. In Hippuris, it appears to result from endogenous cell-formation in the lengthened upper compartment of the original germ-cell.

116. The difference between the development of the pollen grain, and that of the microspore of Selaginella and of the Rhizocarpeæ, is no less remarkable. Among the Phanerogamia, after the pollen grain has remained for some time in contact with the stigma, its inner membrane grows out at one point of its periphery into a filiform cell; this lengthens more or less rapidly until it reaches the micropyle of the ovule, which it enters, and at last comes into contact with the embryo sac. The sac usually resists it strongly; sometimes it is bulged in, but is very rarely perforated. In consequence of this act the transformation of the germ-cell commences. The absence of moving filaments among the higher plants stands connected with the intervention of a second membrane (that of the embryo sac) between the two fluids, the union of which seems to constitute the essential condition of fecundation.

117. In comparing the development of the microspore with that of the spore of the Ferns with which the plants among which it presents itself are so closely allied, the difference is even more striking. In Selaginella all the steps intervening in the Fern between the spore and the tessellar cells of the antheridium have disappeared.

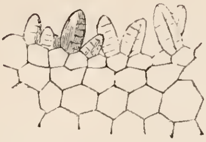
118. Direct observations relating to the act of impregnation among the Cryptogamia, are for the most part wanting. The presence of antherozoids in the cavities of the archegonia of the Ferns has been witnessed only by Suminski and Mercklin. Among the Hepaticæ and Mosses, Hofmeister observed within the involucre of *Jungermannia bivaricata*, antherozoa "which moved rapidly and played livelily round the archegonia."* In this species, as well as in *J. bicrenata* and *bicuspidata*, the same observer found a mucous substance of glass-like transparency, occupying the mouths of the archegonia. In this substance were embedded numerous curled fibres, which he considered to be dead antherozoids. Evidence more to be depended upon is that of the concurrent testimony of all observers that, among the diœcious mosses and liverworts, wherever plants bearing archegonia grow in the neighbourhood of those bearing antheridia, fruits are almost always produced; while in the contrary case, the archegonia are abortive.

119. *Origin and development of germ-cells in special organs destined for their reception, which are capable of transformation into rudiments of new plants, without the concurrence of two organs of opposite functions.*— Of this, distinct examples occur only among the Hepaticæ; viz. among the leafy Jungermanniæ, and the Marchantiæ. In one of the latter, the *Lunularia vulgaris*, there is formed by the doubling in of the epidermal layer of the upper surface of the frond, immediately behind the notch in the anterior margin, a crescentic pouch, which extends backwards for about a line under the surface. Its cavity is bounded by an inferior and a superior wall, whose concave surfaces unite in a sharp margin, the plane of which inclines slightly backwards and downwards. The upper wall is formed by the double epidermal membrane; the lower by a membrane which is intimately united with the parenchyma of the frond, in its relations to which it resembles the tissue which lines the subepidermal air cavities. It consists originally of a single layer of tessellar cells, much smaller than those upon which they are supported. A number of these grow out into papilliform projections, in each of which the projecting hemispherical portion is soon separated by a transverse septum. A second is then formed above the first, and parallel to it. The highest cell next divides by a vertical septum parallel

* Hofmeister, Vergleichende Untersuchungen, &c. S. 38. *Vide supra, Fig.* 164.

to the axis of the frond. This is followed on each side by transverse, and afterwards by

Fig. 200.



Vertical section of floor of gem-pouch of Lunularia, 50 diam.

The club-shaped rudiments of the gems are attached by their bases to the superficial layer of cells, which are much smaller than those upon which they are supported.

vertical septa, which last are parallel to it. Hence results a bilateral organ, the surfaces of

Fig. 201.

Mode of origin of the gem.

Two of the cells of the superficial layer are seen more highly magnified. The membrane of each has grown out into a nipple; in one the vertical septum can be distinguished. 400 diam.

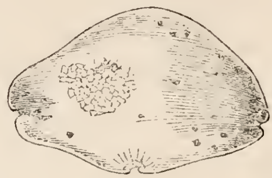
which are at right angles to the axis of the frond. Its form is at first that of a flattened

Fig. 202.

a flattened rudiment of the gem viewed laterally. Division of the second cell of the rudiment by a vertical septum, on each side of which the commencements of several transverse septa are modelled out in the protoplasma. 400 diam.
b, the same at a later stage, 250 diam.

club: afterwards, as it becomes larger, two notches are formed on each of its *lateral* margins, which exactly resemble those of the *anterior* margin of the young frond. As soon as its development is completed—that is, when it has attained a length of about $\frac{1}{3}$ of a line, it is pushed out of the receptacle by its rapidly growing successors. If, after its expulsion, it is sown on a damp surface, a new growth at once commences in two opposite directions, in a line which is at right angles to its axis. At the same time the cells of the inferior surface grow out into nipple-shaped projections, which soon become filamentous roots, and the whole is transformed into a riband-shaped frond. The organ, the development of which is de-

Fig. 203.



Outline of gem as observed two or three days after it has been sown, 50 diam.

In its inferior margin is a notch which indicates its point of attachment to the floor of the gem-pouch. The other two notches, one on each side, are the points of growth of the young plant into which the gem is transformed: they resemble those which are described (§ 58.) in the margins of the young frond of Anthoceros. It is remarkable that the line of direction of growth of the young plant is at right angles both to that of the gem itself, and to that of the parent plant.

scribed above, receives, in common with others of a different nature, the name of "gem." The whole process differs widely from that of true gemmation or "rejuvenescence" of an old cell, in order that its primordial vesicle may be transformed into an embryo. This distinction is well illustrated in the gemmation of Anthoceros; the primordial sac of a cell of the parenchyma of the frond, the position of which is undetermined, contracts and secretes on its surface a new cellulose membrane. The new cell is converted by repeated division into the rudiment of a young frond, which, as it grows, breaks through the tissue of the parent. In Jungermannia bivaricata, we have observed a similar process. A single cell of the leaf of a marcescent, last year's stem, is seen still to contain a primordial vesicle, lined with green protoplasm. This forms around itself a new cell, which divides by a septum, the direction of which is transverse in relation to that of the first growth. One of the resulting cells grows out so as to project through, or carry before it, the membrane of the old cell. This divides by a septum inclined obliquely to the former, which is succeeded by another, inclined in the opposite direction, and so on alternately. Hence results the rudimentary stem of a new plant. Both of the preceding are examples of gemmation.

The very distinct analogies in development (homologies) which present themselves among the higher plants, are exhibited in the following table. The six last vertical columns represent the principal groups, which follow each other in the same order as in the preceding pages. In the two first columns are indicated those more partial analogies which may be traced between the higher plants, on the one hand, and the Algæ, Fungi, and Lichens on the other.

TABLE OF THE ANALOGIES IN THE DEVELOPMENT OF DIFFERENT CLASSES OF PLANTS.

ALGÆ, FUNGI AND LICHENS.	HEPATICÆ AND MOSSES.	FILICES.	RHIZOCARPEÆ.		LYCOPODIACEÆ.		PHANEROGAMIA GYMNOSPERMIA.		PHANEROGAMIA ANGIOSPERMIA.	
	SPORE-CELL.	SPORE-CELL.	MACROSPORE.	MICROSPORE.	MACROSPORE.	MICROSPORE.	EMBRYO-SAC.	POLLEN-CELL.*	EMBRYO-SAC.	POLLEN-CELL.
Germination results in the formation of a Conferva, Mycelium or Hypothallus.	Germination results in the formation of a filamentous Protonema.	Germination results directly in the formation of the	Germination consists of the development within the inner membrane of the spore of the	Germination consists in the bulging out of the inner membrane of the microspore.	Germination as in	Rhizocarpeæ.		Germination represented by the growing out of the inner membrane so as to form the pollen-tube.		The same.
Frond, Receptacle, Thallus.†	Frondose or leafy Stem.	Prothallium.	Prothallium.	Absent.	Prothallium.	Absent.	Absent	Absent.	Absent.	Absent.
Globule of Chara.	Antheridium.	Antheridium.		Antherozoids.		Antherozoids.		Absent.		Absent.
Antherozoids of Chara, Zoospores, Spermatia, &c.	Antherozoids.	Antherozoids.								
Nucule of Chara.	Archegonium.	Archegonium.	Archegonium.		Archegonium.		Corpusculum.		Absent.	
Germ-cell of Chara.	GERM CELL. Divides into two transversely.	GERM-CELL. Mode of division uncertain.	GERM-CELL. Mode of Division uncertain.	:	GERM-CELL. Divides into two transversely and is thus transformed into		GERM-CELL. Divides into two transversely, and is thus transformed into		GERM-CELL. Mode of Division the same.	
	Inferior of the two cells which result from the above division.	Uncertain.	Uncertain.		Suspensor.		Suspensor.		Suspensor.	
	Fruit-stem.	*Embryo*	*Embryo.*		*Embryo.* Cellular Tissue, occupying the cavity of inner membrane of spore.		*Embryo.* Albuminous Body.§		*Embryo.* Endosperm.	
	Spore bearing Fruit-stem.‡	*Spore-bearing plant.*	*Spore-bearing Plant.*		*Spore-bearing Plant.*		*Ovule-bearing Plant.*	*Anther-bearing Plant.*	*Ovule-bearing Plant.*	*Anther-bearing Plant.*
	Sporangium.	Sporangium.	Sporangium.		Sporangium.		Ovule.	Anther.	Ovule.	Anther.
	Primary Parent-cell divides into four special Parent-cells, each containing a *Spore.*	The same.	The same.		The same.			Primary Parent-cell divides into 4 special Parent-cells, each containing a Pollen grain.		The same.

* According to the researches of Dr. Reissek "Uber die selbständige Entwickelung der Pollenzelle zur keimtragenden Pflanze," (Nova Acta Ac. Cæs. *l. c.* t. xxi. p. 468.) the tube which is emitted by the pollen grain of many Phanerogamia, when sown on a moist surface under suitable conditions, develops a new plant, which not only vegetates independently, but bears acrogenous spores at the termination of the filaments of which it is composed. Reissek describes a fungus which results from what he calls the germination of the pollen cell of Caltha palustris, which resembles in every respect a Botrytes.

† The Lichens in general, and especially the gelatinous Lichens (Gallert-flechten, Byssaceæ of Leveillé) exhibit several very remarkable points of resemblance to the Fuci. The structure and arrangement of parts in the conceptacles of the latter, correspond closely with those met with in the apothecia of the former. The large spores of Fucus with the smaller masses (usually eight in number) into which its endochrome is divided previously to its germination, may be compared to the ascus of the Lichen with its eight spores; while the filament bearing Antheridia are represented by similar filaments bearing spermatia.

‡ In some species of mosses, if the plant is transferred into an unusually moist atmosphere shortly after the commencement of the development of the fruit, this last is transformed into a stem bearing symmetrically arranged leaves, thus manifesting a tendency to the higher vegetative development which presents itself in the spore-bearing plant among the ferns.

§ The endospermal tissue of the Phanerogamia appears to us to exhibit a much more distinct resemblance in its mode of origin and formation to the tissue which occupies the cavity of the spore in the Lycopodiaceæ, than to the prothallium itself, which last structure seems to be unrepresented among the higher plants. Hofmeister having taken the opposite view, we express an opinion on the point with hesitation.

‖ The existence of antheridia among phanerogamous plants has been asserted by Grisebach, who has described as such certain bodies occurring in the leaf-buds of various species of Rhamnus. On this subject, see the author's "Note on the supposed Antheridia of Rhamnus," in the Annals of Nat. Hist. for August and September, 1851.

Appendix. — *On the relations which exist between the animal and vegetable kingdoms, as regards the function of reproduction.* In the introduction to the foregoing article, it was observed that, if any analogies in development may be supposed to exist between plants and animals, they are to be sought between the lowest members of the two series. Whether we conclude that it is or is not possible to mark out the limit which separates the one kingdom from the other, it is not to be overlooked that the phenomena of reproduction, and consequently the whole circle of the development, of the zoosporous Algæ resemble more those which present themselves on the other side of the disputed territory, than those which occur among the higher plants. Let us compare the development of a unicellular Alga, with that of one of the simplest Infusoria. An egg-shaped body composed of a homogeneous and contractile substance — as regards its chemical constitution nitrogenous — displays active motions, and exhibits two locomotive organs springing from its smaller end. Soon, however, its motions become languid; a newly formed cellulose membrane, which is not contractile, encloses it, and now it undergoes a kind of cleavage, which results in the formation of a number of new bodies. In each of these, as soon as they escape from the parent, the same transformation is repeated.

In the other case, taking the development of Vorticella as an illustration (in the description of which we follow Stein*), we find that a disc-shaped mass of homogeneous contractile substance (a monad), is transformed into a stalked and ciliated Vorticella. After having been for a time endowed with active motion, and with a power of ingesting food, the Vorticella enters into a state of repose, and at the same time is enclosed in a flexible membrane or cyst. The interior of the cyst is now occupied by a mass of protoplasma, which is no longer contractile, and presents no trace of the structure of the former Vorticella. By a process similar to that which occurs in the plant, this plasma divides into a number of disc-shaped bodies, resembling that from which the parent originated.

Between the Protozoon and the Protophyton, there is an intermediate group, of which the Englena viridis, alluded to in § 1., may be considered as the representative. The Euglena after actively moving for a time, enters into the condition of repose, becoming at the same time enclosed in a new membrane. What follows this change, however, has not been as yet ascertained.

* Stein, Wiegmann's Archiv. für Naturgesch. 1849. Bd. i. p. 92.

The phenomenon of conjugation, also, while it is without parallel among the higher plants, presents itself under nearly similar conditions among the Infusoria. According to the observations of Stein, the circle of changes described in the preceding paragraph, is not the only one by which in Vorticella the specific form is reproduced. A Vorticella enters into a state of rest, and becomes encysted; it is not now, however, converted into a mass of homogeneous protoplasma as in the former case. The cyst membrane changes into a thin walled vesicle, while from the body of the enclosed Vorticella, which has assumed a spherical form, there emanate a number of contractile radiating processes. It is now a Protozoon, identical with that to which has been given the name Actinophrys. Now in Actinophrys, the occurrence of conjugation has been recorded by several trustworthy observers. It was first described by Kölliker*, afterwards by Siebold †, and finally by Cohn. ‡ According to the last-mentioned author, two neighbouring individuals after approaching more and more closely to each other, emit from their opposite surfaces, vesicular processes, which finally unite. As the union becomes more complete, the two seem to form but a single animal. As to what are the results of this remarkable conjugation, neither Cohn, nor, as far as we know, any other observer, is able as yet to speak positively. Every fully formed Actinophrys exhibits embedded in its substance a central nucleus-like body; this nucleus, according to Stein, is sooner or later transformed into an egg-shaped animal, which grows at the expense of the parent, and finally becomes endowed with active motion. At the smaller end is formed a crown of cilia, at the larger an oral depression, and soon there presents itself a perfect Vorticella. It is, at least, extremely probable that this development is the result of the previous conjugation of two Actinophries.

The analogies which have been under our consideration in the preceding paragraphs, may be placed in a clearer point of view, by exhibiting them in a tabular form. Referring the reader to the description contained in §18. of the most simple form of unicellular conjugating Algæ (Palmoglœa macrococca), we shall contrast the circle of development, as it presents itself in Palmoglœa and Protococcus on the one hand, with that of Vorticella on the other, as follows:—

* Das Sonnenthierchen. Zeitschrift für Wiss. Zool. i. p. 198.

† Ueber die Conjugation des Diplozoon paradoxum, u. s. w. *loc. cit.* iii. p. 62, 1851.

‡ Beiträge zur Entwick. der Infusorien, *l. c.* iv. p. 252.

Zoosporous Unicellular Alga.	Conjugating Unicellular Alga.	Protozoon.*
Production of a series of *Zoospores.*	Production of a series of sterile *Podophryæ.*	Production of a series *Monads,* which are transformed into Vorticellæ.
Cessation of motion.		Cessation of motion. Transformation of Vorticellæ into sexual Actinophries.
	Conjugation of two Podophryæ. Cessation of growth.	Conjugation followed by Cessation of growth.

* In the zoosporous Algæ, constantly recurring series of unisexual generations are produced indefinitely. In Vorticella the production of Monads may also recur repeatedly, without the intervention of any sexual stage. So long as this is the case the two developments correspond completely.

Here it may be observed that in the stage of cessation of growth, which, in the Protozoon, as well as in the Protophyton, follows the act of conjugation, we have a condition which corresponds to that of the ovum of the higher animals. The ovum after passing through a period of repose, resembling that which presents itself in Podophrya, exhibits a series of transformations, which correspond to the later steps of the developments under our consideration. This correspondence is, as might be expected, more distinctly seen in the lower than in the higher animals. Thus for example, in the development of a Trematode Worm (Distomum pacificum), the mass of the yolk is transformed into a locomotive rudiment resembling an infusory animal. Within this originates an asexual, but fertile nurse, the homologue of the Vorticella, in the interior of which is formed a second and numerous generation of animals endowed with locomotion (Cercariæ). In these, after a time, the locomotive power is lost, and each finally becomes a sexual Distomum.*

Although the foregoing homologies are founded on observations the details of which are as yet imperfectly worked out (on which account it may seem somewhat premature to draw attention to them), they are not open to the objections which may be urged to homologies supposed to exist between the highest members of the two series. There, the connecting links are wanting; here, we pass through closely related intermediate forms, from the Alga to the Protozoon, and from the Protozoon to the Trematode Worm. Hence, while we are not justified in applying the term ovum to the generative product of the phanerogamous plant, the present state of our knowledge allows us with propriety to compare with the ovum the result of conjugation as it occurs among the Algæ.

The differences in chemical composition which exist between the Algæ and the Protozoa will not serve as a ground of distinction. Euglena is invested during its period of repose with a cellulose membrane and contains granules of chlorophylle. In Polytoma uvella we find, on the one hand, the contractile vesicles of the infusory animal, on the other, starch in the granular form, so characteristic of the plant.†

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The reader is further referred to various researches contained in the 3rd Series of the Ann. des Sc. Nat.

* Carus, "System der Thierischen Morph.," s. 329.
† A. Schneider, "Beiträge zur Entwick. der Infusorien," Müller's Archiv. No. 2. 1854. These researches we recommend to the reader's attention, as containing observations of great importance in relation to the present question.

RESPIRATION.—ORGANS OF. I. *Human and Mammalian.*—The respiratory system of organs in man and mammalia comprehends the larynx, the trachea, and the lungs: embryologically, the thyroid and thymus glands should be included in this category. The embryonic apparatus of the branchial arches falls under the same denomination. In this article the trachea, bronchi and lungs only will be studied, in their general and minute anatomy. These parts in the human subject will be described at length. In mammalia the prominent varieties of structure occurring in some of the commoner genera will be incidentally noticed.

The Lungs (πνεύμων, Gr.; *Pulmo*, Lat.; *Poumon*, Fr.; *Lungen*, Germ.; *Lungs or Lights*, Engl.) coincide typically in structure with the compound grape-like glands. The lobules and air-cells constitute the glandular parenchyma. The larynx, trachea and bronchi represent the excretory apparatus. They differ from all other glands, however, in the mechanism of their action. They simultaneously eliminate and absorb. In the lungs two diametrically opposed functions proceed in the same place at the same time. This mechanical paradox occurs in the example of no other gland. Secretion and excretion are successive steps of the same process. They are not contrary functions. The whole mass of the blood passes through the lungs: other glands receive only a part. The air-passages and cells are far more capacious than the corresponding parts of other glands. This characteristic results from the aeriform nature of the compounds emitted and received. Aeriform bodies are subject to rapid variations of bulk; fluids undergo no material changes of volume, through fluctuations of temperature; thence, in the instance of the lungs, results the necessity for mechanical provisions, which in ordinary glands would exist to no purpose. The elastic tissue and resilient cartilages so abundantly introduced into the structure of the air-passages and cells realise the required provision. The excretory ducts of all other glands are membranous, the opposite sides of which are capable of collapsing into contact. Fluid in motion readily forces its way through a collapsed tube: air can only traverse a patulous channel.

In man the lungs are two in number. They are contained in the cavity of the thorax, one on either side of the spine, and embraced by, but still exterior to the pleura. The *pleura pulmonalis* and *pleura parietalis* are everywhere and always in actual contact. It follows that the space of the thorax must be at all times perfectly filled by the lungs and other organs. In figure each lung is conical. The right is wider and shorter than the left, a difference which results from the position of the liver on the right side and the heart on the left. The right lung is cut by deep fissures into three *lobes;* the left only into two. The base of each lung presents downwards, and rests on the diaphragm; that of the right is more concave than that of the left. On the right side the liver bulges upwards, encroaching upon the chest. The anterior edge of the right lung slopes off obliquely downwards and backwards, so that it projects much lower by its posterior than by its anterior border. On the left side the heart occupies the space which, in the absence from this place of this organ, might have been engaged by a third lobe.

The *apices* of the lungs project above the level of the first rib. The right is higher than the left. The dorsal aspect of the lungs, thick, round, and vertical, is received into the hollow of the ribs near the vertebræ.

It is longer than the anterior. The posterior and inferior margins descend into the angular space between the ribs and the diaphragm. The anterior border is thin, irregular, and oblique. That of the left extends forwards over the pericardium. The inner surface of each lung presents towards the mediastinum. That of the left is hollowed out to receive the heart. The *root* of each lung is attached to the *posterior* edge of its inner surface. Each lung is divided into lobes by fissures, which commence near the apices, and descend obliquely forwards, to end in the anterior border near the base. The fissure divides the lung, on either side, into an upper small lobe and a lower large one. In the right lung a second small fissure is directed downwards and backwards from the anterior margin, to end in the great fissure—it cuts off a small triangular piece from the upper lobe, and gives three lobes to the right lung.*

From Malpighi to Reisseissen, comprehending the first historical period of Anatomical Science, the structure of the lungs formed a constant ground of controversy. From Reisseissen (1803) to Rainey, Addison, Rossignol, Schultze, Moleschott, and Adriani, the most recent authors, differences on this subject have continued to divide the opinions of anatomists. This question, which involves so much that is historically interesting in anatomical science, divides itself naturally into two primary departments: 1st, *the descriptive and structural;* and 2nd, *the historical bibliography.*

The Trachea in man extends from the larynx† to the bifurcation of the tube into the right and left bronchi; its first superior ring, which is attached to the cricoid cartilage, coincides with the upper border of the body of the fifth cervical vertebra: the point of its bifurcation in the thorax is level with the superior edge of the body of the third dorsal vertebra: it averages in internal diameter from $\frac{3}{4}$ of an inch to 1 inch, and in length from 4 inches to $4\frac{1}{2}$ inches.‡ Variations in the length of the trachea are due to the great

* For a full account of the relations of the lungs to the thorax and to the neighbouring viscera, see art. Thorax.

† See Art. Larynx.

‡ "Trachea, $3\frac{1}{2}''$—$4\frac{1}{2}''$ longa, $8'''$—$12'''$ lata, et e pariete anteriore ad posteriorem, $7'''$—$9'''$ ampla est."—Disquisitiones de Structura et Textura Canalium aeriferum. Scripsit Ernestus Schultze. Mitaviæ et Lipsiæ, 1850.

range of motion within which the larynx is capable of changing place. The diameter of this tube is greater in the male than in the female, at the lower than the upper extremity; it is nearly cylindrical in figure, and permanently patulous. It is composed in the human subject generally of about eighteen cartilaginous rings; of these rings the posterior fourth is deficient; the circle is completed at this interval by a musculo-membranous structure. The tracheal muscle stretches from one extremity of each cartilaginous ring to the other: the trachea is therefore contracted in diameter by muscular action, and enlarged by the elasticity of the ring-cartilages. The rebounding property of these cartilages results physically from their ring-like figure: they tend constantly to straighten themselves; this perpetually acting force preserves the patency of the tube. The convexity of the tracheal rings is directed forwards, the membranous interval being placed posteriorly: by this arrangement the exemption of an important organ from external injury is secured. Against the accident of occlusion during the movements of the neck artful provision is made in the flexible and elastic nature of the structures by which the rings are tied together.

The trachea externally is everywhere embraced in loose areolar tissue: upon this circumstance depends the great range of its longitudinal mobility. Its posterior aspect is in contact with the œsophagus, which is interposed between it and the vertebral column. The recurrent laryngeal nerve, ascending to the larynx, is placed in the interval between these tubes.

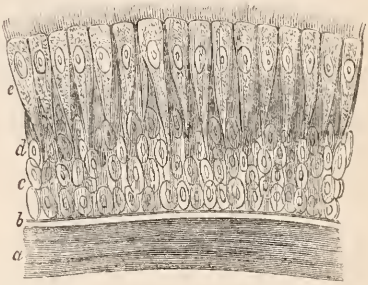
In front of the trachea are situated the sterno-thyroid and sterno-hyoid muscles, which leave an interval in the median line, through which the deep cervical fascia enters to embrace the windpipe. The brachio-cephalic and left carotid arteries, leaving the chest through the episternal notch, lie on the trachea near the top of the sternum: above this limit is observed the plexus of the inferior thyroid veins, and near the larynx it is crossed by the isthmus of the thyroid body: on either side and parallel to it are the carotid vessels and the lobes of the thyroid gland. Entering the limits of the thorax, the trachea is in relation anteriorly with the first piece of the sternum, and the sternal extremities of the sterno-hyoid and thyroid, and to the left, in a descending order, with the innominate vein, the commencement of the innominate and left carotid arteries, which tend towards the sides of the tube, with the arch of the aorta and the deep plexus of nerves, and at the point of its bifurcation it is in contact with the pulmonary artery at the place at which this vessel subdivides into branches. Lying between the two pleuræ, the trachea is contained in the posterior mediastinum; on its right side it is in relation with the pleura and pneumogastric nerve, and on its left, with the carotid artery, the pneumogastric, recurrent and cardiac nerves.

Structural anatomy of the trachea.— The trachea is constructed of cartilage, yellow and white fibrous tissue, muscular fibres, blood-vessels, lymphatics, and glandules, the whole being internally lined by a dense stratum of ciliated epithelium.

These parts may best be described from within outwards.

The tracheal mucous membrane is a development of the pharyngeal. (Henle). It forms a

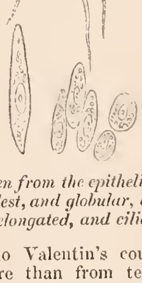
Fig. 204.



Vertical cutting through the epithelial and sub-epithelial layer of the trachea. (After Kölliker.)
a, *b*, basement or homogeneous membrane; *c*, the first race or growth of epithelial cells; *c*, *d*, the last, further evolved; *e*, the adult, surface, ciliated cells.

layer of 0·024—0·04‴ in thickness; it resolves itself into two distinct layers, including severally two equally distinct orders of cells; the undermost, resting immediately on the basement membrane, is composed of orbicular and fusiform particles, measuring from 0·004 to 0·005‴, and bearing a clear conspicuous nucleus of from 0·0025 to 0·003.‴ The superficial stratum is constituted of the adult cells; they consist of club-shaped bodies, armed at the free outermost end with cilia (each single cell carrying about 50 cilia)*, and elongated at the proximal end into a long tapering tail: in length these cells average

Fig. 205.



Separate cells taken from the epithelium of the trachea, the lowest, smallest, and globular, being the youngest; the uppermost, elongated, and ciliated, the oldest.

* According to Valentin's counting, each cell supports no more than from ten to twenty-two cilia; but I have often reckoned many more.

from 0·015 to 0·02‴, and in breadth from 0·0025 to 0·004‴, according to the measurements of Kölliker.* This order of ciliated cells is disposed upon a bed of cytoblasts in a double stratum of about 0·006 to 0·01‴, in thickness: they differ from ordinary cylinder epithelia in the remarkable length to which the attached extremity is prolonged; the tail of each cell exhibits quite the character of a yellow filament, and measures from 0·024 to 0·027‴ in length.

In the centre of the broad end of each of these cells is contained, without exception, a clear, bright, oblong nucleus, of from 0·003 to 0·0045‴ in length; and, further, each nucleus bears a very visible nucleolus (*e*, *fig.* 204.). The cell contents consist of minute granules and fat molecules. Valentin describes a double nucleus in many of these cells.

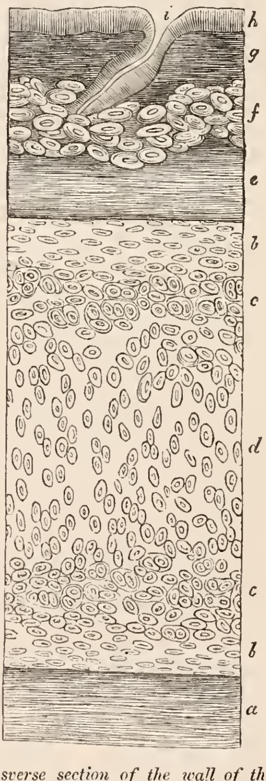
The *cilia* attached to the tracheal epithelium are clear, fine continuations of the cell-membrane: they measure 0·0016 to 0·0022‴ in length: each cilium tapers to its free extremity, that is, it is broader at its base than at its apex. The cilia of the tracheal epithelium are longer and more conspicuous in the embryo than in the adult: the current excited by their vibration tends in the direction of the laryngeal outlet of the tube. Proofs will be afterwards adduced that these motive organules enact no part in the office of respiration: they subserve a merely mechanical purpose in the process of mucous excretion. These epithelia swell in water, while chromic acid restores them to their original characters (*Hannover*). By Biermer and Gosselin †, the tracheal cilia have been detected in motion 78 hours after death in man. Under normal circumstances no *shedding* occurs in the epithelium of the air-passages.

In disease, however, these cells abundantly desquamate. (See Pathological Anatomy of the Lungs).

It thus appears that the cells of the tracheal epithelium proceed from the basement membrane (*b*, *fig.* 204.) in the direction of the surface in successive generations, the youngest (cytoblasts) being the deepest and the next to the blood-supply, and the oldest, the highest and cilia-bearing. It is stated by Hannover ‡, that this epithelium may be indefinitely preserved in chromic acid.

The tracheal glands are productions of the mucous membrane of the trachea. The largest and most numerous are situated in the posterior wall of the tube, and possess long excretory ducts (*i*, *fig.* 206.), which traverse the whole thickness of the muscular and elastic layers. The glandules themselves are best examined from the outside, and rest on the posterior surface of the trachealis muscle; they exhibit a slightly reddish colour, and belong to the compound order of glands (*f*); they do not all belong to the same variety; some coincide in structure with the salivary glands, others with the sudoriferous. Those which are found over the cartilaginous anterior three fourths of the tracheal walls, are thinly distributed, and penetrate into intervals between the ring-cartilages. This class of glands measures from $\frac{1}{10}$ to $\frac{1}{4}$ of an inch: they are smaller than those which cluster on the posterior surface of the tracheal muscle and which measure from $\frac{1}{4}$ of an inch to an inch. In external characters these glands correspond with the grape-like compound glands: from the latter, however, they differ in some particulars. It is only the larger variety of these glands which is lined at the terminal gland-vesicles, with globular epithelium, the ducts being clothed with the cylinder variety. The smaller sort, conforming in this respect with ordinary sudoriferous follicles, are lined throughout with cylinder epithelium. In these latter there is no distinction (*except that of size*) between the epithelium which clothes the blind extremities of the follicles and that which covers the ducts. These follicles fork at their cœcal extremes, each branch measuring from 0·02 to 0·03‴ in

Fig. 206.



Ideal transverse section of the wall of the trachea. (*After Kölliker.*)

a, areolar tissue embracing the cartilages externally; *b*, *c*, *d*, ring cartilage seen in section; *b*, outermost layers having flat cells; *c*, soft and mid-portion — cells oval; *d*, innermost layers with flat cells; *e*, sub-mucous tissue; *f*, part of a tracheal gland; *g*, elastic tissue with longitudinal fibres; *h*, ciliated epithelium.

* Handbuch der Gewebelehre, &c., p. 450.

† Verh. der Wurzb. Phys. et Med. Gesellsch. i. 212.

‡ Müller's Archiv, 1840.

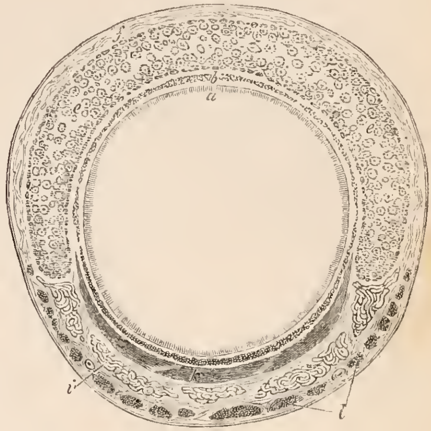
diameter, the parietes of which are composed almost exclusively of fine small cylinder epithelium.

The cylinder epithelium of the ducts of these glands bears no cilia; a character in which it differs from that of the mucous membrane of the trachea in general. The ciliated variety ceases at the orifices of the ducts. The secretion of these glands is a limpid, non-corpusculated fluid. Here it is certain that the act of secretion is not synonymous with that of the shedding of the epithelium. Under certain pathological conditions the tracheal glands augment in size, and become choked with epithelial cells.*

Fibrous Structures. — In the order from within outwards is next observed a remarkable layer of elastic tissue. It lies immediately underneath the mucous membrane (*a, fig.* 204. ; *e, fig.* 206.). It consists of two varieties of fibre, the yellow and the white. The former lies chiefly on the posterior wall, over the trachealis muscles. Its fibres are here disposed in a regular longitudinal direction. They are gathered into thick bundles readily seen with the naked eye, even through the mucous membrane, of $\frac{1}{12}$ of an inch in thickness. They descend in a serpentine manner along the posterior aspect of the trachea, and will be afterwards traced on the bronchi. They frequently anastomose. Smaller fibres, forming a thinner layer of the same tissue, are distributed over the anterior walls of the trachea; like the former portion, running under the mucous membrane and preserving uniformly a longitudinal course. Another order of elastic tissue lies between the ring-cartilages, tying them together cylindrically. Of this tissue the fibres are more slender than those of the former, and belong to the white variety (Bowman). It is to the elastic property of this tissue that the trachea owes its power of lengthening and shortening, a power which in birds is more remarkable than in mammalia.

The *tracheal cartilaginous rings* come next to be described. Each cartilage forms a little more than three quarters of a circle (*e, fig.* 207.). It embraces the anterior three-fourths of the tracheal tube. The deficient portion, comprising the remaining fourth of the circle, is completed by muscle and membrane and elastic tissue (*k, fig.* 207.). This description applies only to the case of the human subject. In the sheep the posterior

Fig 207.



Transverse section of the trachea through the middle of (and parallel with) one of the cartilaginous rings. (After Schultz.)

a, ciliated epithelium, lining the inside; *b*, elastic longitudinal tissue; *k*, the tracheal muscles; *e*, ring cartilage; *f*, external areolar tissue; *i*, blood-vessels; *l*, tracheal glands.

ends of the tracheal cartilages meet, to project behind as spinous processes, thus concealing the trachealis muscle. In the horse the same parts of the ring cartilages overlap. This arrangement prevails also in the dog. In the ox the posterior ends of the tracheal rings are everted. Each cartilage is embraced in a fibrous perichondrium (*f, fig.* 207.) which is intimately united to the inter-annular fibrous tissue.

In ultimate structure these cartilages are chiefly composed of cells interspersed through a fibrous basis (*b, c, d, c, b, fig.* 206.). The cells are largest and doubly nucleated in the centre of each cartilage (*d*). At the inner and outer surface these cells become flattened and elongated (*b, b*). In different parts of a vertical section of the cartilage they present different directions as regards their long axes (*d*). They are charged, in addition to the nucleus, with minute fat molecules. The first and last rings of the trachea are figured differently from the rest. The first constitutes a complete ring of cartilage, and is frequently anchylosed to the cricoid. The last is prolonged backwards over the membranous interval ; consisting of more than one piece, it arches over the angle where the trachea bifurcates into the primary bronchi. By such skilful adaptation of these elastic rings, the occlusion of the air-tube is prevented during the varied motions of the neck and chest. Unlike the laryngeal cartilages, the tracheal manifest no disposition to ossify. They amount, in man, to from 16 to 20 in number, and measure each in width, from above downwards, about one line and a half. They frequently fork at their posterior

* "Die Drüsen des Kehlkopfs und der Luftwege überhaupt werden bei Catarrhen häufig verändert, so dass ihre Bläschen bis 0·08 selbst 0·15‴ messen und mit kleinen rundlichen Zellen erfült sind, die wohl den auf Schleimhautoberflächen sich bildenden Schleimkörperchen sich vergleichen lassen."—Kölliker, Anat. Mik., p. 452.

"Interdum hæ cryptæ mucosæ amplificatæ, ita ut pæne 1‴ latæ sint, et sinubus secundariis instructæ reperiuntur. In hoc casu illæ sæpe usque in regionem plexuum vasorum postea et porriguntur. In preparatis per longum tempus in spiritu vini asservatis aperturæ harum cryptarum mucosarum nudis oculis optime cerni poterant, atque imprimis numerosæ in parietis anterioris interstitiis non cartilagineis et in pariete posteriore animadvertebantur."—Disq. de Struc. et Text. Canal. aerif. S. E. Schultze, 1850.

extremities, and sometimes two or more become united. The internal aspect of each ring is thickened into a rounded form. This disposition of material exhibits an advantageous mechanical adaptation to the chief purpose which these cartilages are designed to fulfil. It confers upon them a powerful *straightening* tendency. To this continuously-acting mechanical force the trachea owes its patency. If the membranous interval of the tube be suddenly cut longitudinally, the rings will rebound almost into straight lines.

The *tracheal muscles* (*k*, *fig*. 207.) extend transversely between the free ends of the ring-cartilages, and also in part *between* these rings in form of oblique fasciculi, a disposition which enables them to influence both the transverse and longitudinal movements of the tube. The fibres of each muscle do not extend in a regularly parallel direction from one extremity of the ring-cartilage to the other. They interweave frequently and irregularly. They are also intermixed with elastic tissue. They form a layer of 0·3′′′ in thickness. The elements of each fascicle are 0·03′′′ long, and from 0·002 to 0·004′′′ broad. Along the course of the fibres, at long intervals, are observed nuclei of very elongated figure.

The tendon of each muscle is attached to the internal surface of the ring cartilage, at some distance inwards from its extremities. This arrangement confers upon the muscle great mechanical advantage in the act of narrowing the tube. In the horse, this disposition of the tendons is still more marked. In man and mammalia the tracheal muscles belong to the *unstriped* variety. In birds they are striated: this is also the case in the muscles of the snake. The layer formed by these muscles is perforated by the ducts of the tracheal glands, which are thickly distributed over its posterior surface in form of reddish granules (*l*, *fig*. 207.).

The musculo-membranous portion of the trachea in man is narrower at the laryngeal end of the tube than at the thoracic. Above, *less* than one third of the circumference of the cylinder is membranous; below, *more*, except at the actual point of bifurcation. The tracheal glands are more numerous at the thoracic than at the laryngeal end. At the former point, both the vascularity and sensibility of the tube are greater than at the latter. It is the innermost and immediate inlet into the organs of breathing. Here, in man and mammalia, the excitability and high organisation of the larynx are repeated, and in birds a second larynx is developed. The presence of mucus at this point excites immediate cough. The trachea is to the lungs as the apex of a rapidly-expanding cone is to its base.

The *arteries* (*i*, *fig*. 207.) of the trachea are chiefly derived from the inferior thyroid, and the *nerves* from the sympathetic and the recurrent of the pneumogastric. By injection it is easy to demonstrate the existence of a submucous capillary plexus.

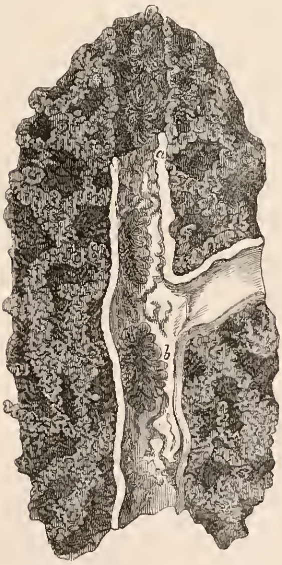
The meshes of the web are considerably larger than those of the true pulmonary plexus. A network of lymphatics also exists in the submucous tissue of the trachea. The meshes of this web are larger and more round-angled than those formed by the blood-vessels.

The *Bronchi* are the primary divisions of the trachea. They consist of two single tubes, one on either side, leading to either lung. Immediately on entering the substance of the lung, they undergo divisions into as many branches as there are lobes. The bronchus on both sides is posterior to the vessels at the root of the lung, and is surrounded by the bronchial vessels and glands and by the pulmonary nerves. The right bronchus presents a greater diameter than the left; it is shorter than the latter, and passes almost horizontally outwards above the right pulmonary artery, and the vena azygos arches over its upper part. The left bronchus, nearly double the length of the right, passes obliquely downwards through the arch of the aorta, and, in its extension to the lung, lies on the œsophagus, thoracic duct, and descending aorta, being below the level of the pulmonary artery. The right and left bronchi, *before* they penetrate the pulmonary substance, exhibit the same structure as the trachea. The cartilaginous rings are imperfect behind, like those of the trachea; the interval being completed by a musculo-membranous structure. These cartilages on the right bronchus vary from six to eight in number, being shorter and narrower than those of the trachea. Those of the left amount to from nine to twelve. The membranous posterior space is thickly interspersed with glands like those of the trachea. *After* entering into the substance of the lungs, the bronchial tubes become modified in structure. The cartilages are no longer parallelly disposed semi-rings. They are arranged in irregular curved pieces over every point of the circumference of the tubes. They do not exist in the corresponding part of the bird's lungs. Thus the bronchi may be classified as the *extra* and *intra* pulmonary.* Compressed at every point of their circumference by the surrounding pulmonary substance, it is evident that the tubes *within* the lungs should be constructed such as to be capable of resisting external pressure. This provision is adroitly realised in the manner in which the cartilaginous pieces are disposed over the walls of the tubes. Each piece of cartilage, having a main circular arrangement, is a small segment of a large circle. They are tied together by muscular and elastic fibres. Thus they form a patch-work, cylindrical frame. The diameter of the tubes is diminished by the approximation of the separate pieces under muscular agency. The patency of *these* tubes, unlike that of *those* of which the walls are exclusively membranous,

* By some authors the air-tubes within the lungs are distinguished as the *bronchia* and *bronchiola*, after Haller, who thus alludes to them:—"Eos ramos Veteres *bronchia* syringes et aortas dixerunt."—Elem. Phys.

is not the result of atmospheric pressure, nor of the action of the thoracic inspiratory muscles: it is due to the elastic property of the cartilaginous pieces. A "membranous interval" in the walls of the intra-pulmonary bronchi would obviously expose the air-passages to injurious pressure. The muscular fibres which always belong to the unstriped kind in this class of bronchial tube are arranged chiefly circularly, but partly longitudinally. They are thus enabled, not only to contract the calibre, but *to diminish the length*, acting, therefore, as important expiratory powers. As the dissector advances towards the branches of the "bronchial tree," the cartilaginous fragments in the walls of the tubes become thinner and smaller, and more and more distantly placed, until eventually they cease altogether, the walls of the tubes being composed of nothing but fibro-membrane. Here the tubes are maintained in the open state in part by the expansive force of the contained column of air. The collapse of these passages leads to the *ataleclasis* of that portion of the lung to which they lead. At this point the gravest impediment to respiration, in *bronchitis*, occurs; here also is chiefly seated the obstacle to expiration in some forms of emphysema; and these musculo-membranous tubules are the scene of spasm during the paroxysms of spasmodic asthma. The parietes of the bronchial tubes

Fig. 208.



A section of a minutely injected piece of human lung. (After Rainey.)

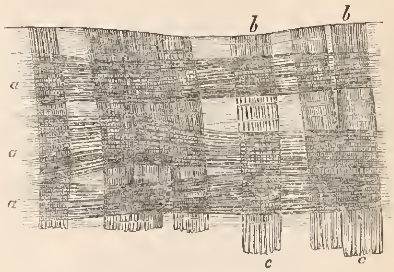
The section cuts longitudinally a branching bronchial tube. At *a*, the ciliated *epithelium* of this tube is seen to terminate by an abruptly defined border, illustrating the doctrine held by Mr. Rainey, which contends for the complete absence of *all* epithelium from all parts of the lung beyond this limit. *b* marks the sudden manner in which the intercellular passages arise from the extreme bronchi.

within the substance of the lungs bear glands like those of the trachea, and, like the latter, they are lined internally by a ciliated cylinder epithelium. *This* epithelium terminates, by abruptly-defined borders, at the commencement of the true pulmonary tissue. (*a*) This fact was first shown by Mr. Rainey*: subsequent observers have, however, proved, contrary to the opinion of Mr. Rainey, that the epithelial layer does *not wholly cease* at these points (*b*). It is prolonged over the respiratory segment under the character of pavement-epithelium.

The true bronchi, in every part of the lung, are distinguished by their tubular form and smooth walls (*a*, *b*) — characters in which they contrast with the loculated aspect of the intercellular passages.

The walls of the minutest bronchi are composed of three coats: a mucous, a muscular, and fibrous. Schroeder van der Kolk has proved that unstriped muscular fibres are contained in the parietes of the smallest of these tubes. The illustrations which accom-

Fig. 209.



Sub-mucous tissue from a small bronchial tube in the human lung. (After Harting.)

a, *a*, *a*, elastic longitudinal fibres blended with muscular bands; *b*, *b*, muscular fascicles disposed circularly; *c*, *c*, extremities of the same, showing the *absence of tendons*.

pany the theses of Adrius Adriani are drawn by S. van der Kolk himself, from his own microscopic dissections. In the whale, the structural elements of the walls of the smallest bronchial tubes are of very large dimensions, and therefore readily to be detected.

The muscular fibrillæ are principally disposed circularly (*b*, *c*, *b*, *c*); and the elastic (*a*, *a*, *a*), longitudinally.

During the *ingress* of the respiratory column of air into the lungs, both these orders of fibres must be stretched; during the egress of the air, the one must actively contract, the other must passively recoil. This constitutes an expiratory force. It is important to remember that these two elements continue to prevail in the parietes of the bronchi as long as they retain the character of bronchi properly so called — in other words, to the limits everywhere which denote the origins of the intercellular passages. At this point the muscular element ceases altogether; so also does the *ciliated* epithelium; but the elastic

* Med. Chir. Trans. vol. xxviii., 1845.

fibres proceed, under a modified form however, over the walls of the intercellular passages and air-cells. The muscular and fibrous structures are discoverable in the walls of the bronchi *after* these latter have penetrated within the bounds of the lobuli; but never the cartilaginous. This latter element, however, exists in the walls of the smallest of the extra-lobular bronchi.

The extreme end of each bronchus is the common mouth of the *infundibulum* of Rossignol; the peduncle of the pulmonary vesicles of Reisseissen; the origin of the interlobular passages of Addison.

The *bronchi divide on no constant or regular plan.* — Small branches sometimes proceed from a large stem, at different angles, from every point of its circumference.

Fig. 210.

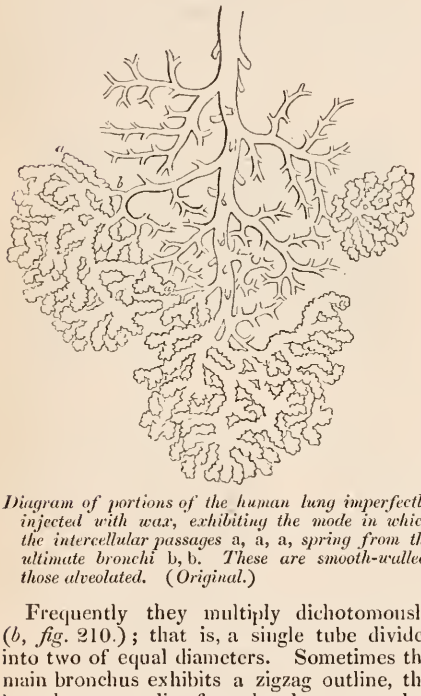


Diagram of portions of the human lung imperfectly injected with wax, exhibiting the mode in which the intercellular passages a, a, a, *spring from the ultimate bronchi* b, b. *These are smooth-walled, those alveolated.* (*Original.*)

Frequently they multiply dichotomously (*b*, *fig.* 210.); that is, a single tube divides into two of equal diameters. Sometimes the main bronchus exhibits a zigzag outline, the branches proceeding from the alternate angles. This latter method obtains with great constancy in the case of the intralobular bronchi. The number of branches *within* the lobule into which a bronchus subdivides bears a general proportion to the size of that lobule. In the smallest, the intercellular passages begin from two or three bronchial peduncles; in the largest, from eight or ten. In some instances a second or supplementary bronchus enters a lobule at the side. It is, however, the rule, that each lobule is supplied only with a single central bronchus. The point of attachment of the bronchus is the *apex* (*a*) of the lobule (*b*); the opposite point being the base. The angle of division in the bronchial tree is, for the most part, the *obtuse.* This disposition of the tubes favours, mechanically, both the ingressing and the egressing column of air.*

It has been maintained by Dr. Radcliffe Hall†, that the contractility of the bronchial tubes is called into action rhythmically in each expiratory movement, to assist in emptying the lungs. But no evidence has been adduced in support of this doctrine. If the contraction of the bronchial tube, through muscular or any other force, occurred at the first stage of the act of expiration, it is obvious that it would arrest rather than favour the egress of the air. It is not, however, improbable, that a certain *regulated* power over the outgoing column of air is exerted by the parietes of the bronchial tubes. This is more likely to consist in a shortening and lengthening of the tubes. They may also serve to regulate the supply of air to the lobules, in accordance with the wants of the system, just as the contractility of the minute arteries regulates the supply of blood to the organs to which they proceed. ‡ It may possibly be through this channel that the remarkable variation is effected in the amount of respiration which adapts the quantity of heat produced to the depression of the external temperature. It has been further suggested by Dr. W. Gairdner § that the contractility of the smaller bronchi may serve to expel collections of mucus which may accumulate within them, and which neither ciliary action nor the ordinary expiratory efforts suffice to displace.

Ultimate pulmonary tissue. — Lobules. — Historical bibliography. — From the dawn of anatomy to the present age, "the structure of the lungs" has proved a fertile theme for disputation. Anterior to the era of Malpighi, anatomists were wont to regard the lungs as consisting of "a spumous tissue," in which air and blood became directly intermixed. Malpighi ‖ first demonstrated the untenableness of this view. He placed the fact beyond doubt, that the air and the blood were contained in *separate* channels.¶ He described the air-cells, and contended that they communicated among themselves, but not with the blood passages.

In the year 1665, Bartholin wrote to de-

* "Rien n'est plus varié que la longueur de ces rameaux, le mode de ramification qu'ils subissent, le nombre de leurs subdivisions et la direction que celles-ci affectent. On peut cependant les rapporter à deux types principaux: le premier comprend les tubes aériens qui sont soumis au mode de division par ramifications alternes; le second, ceux qui subissent la loi de dichotomie ou de trichotomie."—Recherches sur la Structure intime du Poumon de l'Homme, &c. par M. Rossignol. Bruxelles, 1846.

† Trans. of Prov. Med. Assoc. 1850.

‡ Carpenter, Principles of Human Physiology, p. 514.

§ Edinburgh Monthly Journal, May, 1851.

‖ Marcellus Malpighi, Opera omnia, Lugd. Batav. 1687, p. 320. Lettre première.

¶ "Ex trachea in ipsas mox ex una in alteram patens sitaditus et tandem desinent in continentem membranum."

fend the theory of Malpighi.* Willis † came next in the list of disputants. By him it was argued, that the extreme bronchi deprived of their cartilages *bulged on all sides* into the "vesicles" described by Malpighi, and that they communicated among themselves. After Willis came Borel ‡, and Duverney. § By the former it was denied that muscular fibres exist in the walls of the vesicles; by the latter it was maintained that the extremities of the bronchi in man's lungs, as in that of the bird, communicated amongst themselves.

Helvetius (1718) ‖ now sought to modify the views of Malpighi as developed by Bartholin and Duverney. He also admits that the pulmonary tissue consists of a cellular or spongy tissue, of which the cells open the one into the other.

Haller ¶ now entered the arena. This illustrious anatomist doubted the existence of a system of air-cells in the lungs, because he could not see that those of one *lobule* were connected with those of the adjacent. Haller, at this period, was followed by Hales, Volelfart, Hamberger, Hildebrand, each in his turn advocating some modification of the opinions already stated.

A new epoch now occurred in the history of this controversy by the publication of the far-famed "*Dissertation*" of Reisseissen.** In the judgment of the Berlin academicians the researches of Reisseissen overthrew, by undeniable fact and experiment, the theories of Willis, Malpighi, and antiquity. It was taught by Reisseissen, that the air-cells form the real terminal extremities of the bronchial tubes, each vesicle being independent of the others, and having its own separate bronchial peduncle.††

In 1825, Magendie published opinions with reference to the structure of the lungs, which were essentially a reproduction of the views of Helvetius.‡‡ The facts adduced by Magendie did not, however, satisfactorily overthrow the theory of Reisseissen. In England, Home and Bauer §§, attempted at this period to show that the pulmonary vesicles did not consist of dilated air-tubes, as supposed by Willis and Reisseissen, but of polygonal cells of determinate form. They declared a preference for the theory of Malpighi. M. Bazin, in the year 1832 *, reproduced the opinions of Reisseissen. In 1839, M. Sereboullet † followed on the same side. About this period, M. Bourgery in France, and Dr. W. Addison in England, combated severally the views of Willis and Reisseissen. To the theories of these anatomists, more especial reference will be afterwards made. Dr. Addison ‡, from a repetition of the method adopted by Reisseissen, concludes, "that the bronchial tubes, after dividing into a multitude of minute branches, which take their course in the cellular interstices of the lobules, terminate in their interior in branched air-passages and freely communicating air-cells." Mr. Rainey, whose excellent memoirs have rendered great service to the cause of the minute anatomy of the lungs, more clearly defines the distinction between the inter-cellular passages (the *lobular passages* of Drs. Todd and Addison) and the true bronchi.§ M. Hüschke ‖ in 1844 published researches which tended to support the views of M. Bourgery. At this time Dr. Eichholtz ¶ contributed to anatomy the results of careful investigations into the structure of the lungs. The dissertation of Dr. Moleschott ** was also added to the rich list of works on the organisation of these parts. The views of this excellent writer differ in no essential respects from those of M. Rossignol ††, who describes the extreme bronchi as terminating in *infundibula*, which sacculate into *lateral* and *terminal alveoli* (air-cells). In the year 1848, Adrius Adriani ‡‡ published a dissertation of considerable value. It is illustrated by drawings taken from their own preparations by Schrœder van der Kolk and Harting. To this admirable essay, special allusions will be afterwards made. An inaugural dissertation, also, by Ernest Schultz §§, devoted chiefly to questions of structural anatomy, now appeared to enrich the literature of this subject.

The standard writings of the English anatomists issued at this period express chiefly the views of the continental authors above quoted. In Carpenter's Principles of Human Physiology, and Messrs. Todd and Bowman's Physiological Anatomy, excellent chapters

* Bartholin, De Pulmonum Substantia et Motu Diatribe. S. 1. p. 355 of the edition added to the works of Malpighi, Op. Om. &c. 1687.

† Willis, Thomas, Opera omnia, "De Respiratione et Usu," p. 8. Genev. 1680.

‡ Borel, De Motu Animantium, pars secunda. Hagæ, Com. 1743.

§ Mémoire de l'Académie des Sciences, 1718, quoted by Reisseissen, De Pulmonis Structura. Argent, 1803.

‖ Mémoires de l'Académie royale des Sciences, année 1718, p. 22. tom. i.

¶ Elementa Phys. Corp. Humani. Laus. et Bern. 1761, t. 3. et p. 178.

** Op. cit.

†† "Extremi surculi cylindri sunt ut reliqui rami, sed brevissimi, nec sphæricas vesiculas nec polyedras, nec cubicas referunt."

‡‡ Leçons sur les Phénomènes Physiques de la Vie, ii. 37.

§§ Phil. Trans. 1827.

* Comptes rendus de l'Académie des Sciences, la Structure intime du Poumon. Paris, 1832.

† Sereboullet, Anat. Comp. de l'Appareil Respir. Strasbourg, 1838.

‡ Phil. Trans. 1842.

§ See his Memoirs "On the Minute Structure of the Lungs," 1845; "On the Minute Anatomy of an Emphysematous Lung," 1848; and "On the Minute Anatomy of the Lung of the Bird," in vols. xxxii. and xxxiii. of Medic. Chir. Trans.

‖ Sömmering's Lehre von den Eingenweiden (etc.), p. 268.

¶ In Mullen, Archiv, fur Anat. und Physiologie, Heft V.

** De Malpighianis Pulmonum Vesiculis. Heid. 1845.

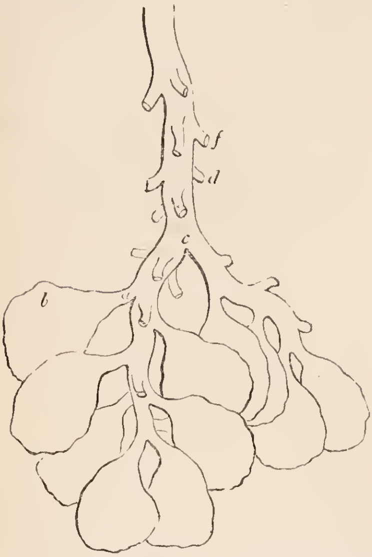
†† Récherches sur la Structure intime du Poumon de l'Homme et des principaux Mammifères, &c. 1846, Bruxelles.

‡‡ Dissertatio Anatomica Inauguralis de subtiliori Puulmenum Structura. Trajecta ad Rhenum, 1848.

§§ Disquisitiones de Structura et Textura Canalium aeriferorum, &c. 1850, Mitavæ et Lypsiæ.

will be found on the structure of the lungs. The works of the Würzburg Professor (Kölliker) contain the most recent, and probably the most conclusive and important, researches upon this subject.* In the details which are now to follow reference will be frequently made to the views taught by this distinguished anatomist.

Fig. 211.

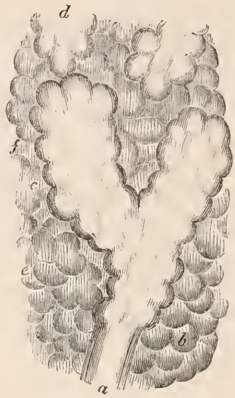


A group of lobules loosened from their mutual attachments, indicating the mode in which each lobule (b) *receives a single bronchial tube* (a). (*Original.*)

At *c* is represented the dichotomous manner in which the primary and secondary orders divide; at *c*, *d*, and *f*, is shown the irregular arborescent method in which the terminal lobular bronchi project from every side and point of the circumference of the secondary bronchial tubes.

Minute Anatomy of the Lobule.—The proper pulmonary tissue (*b*, *fig.* 211.) begins where the bronchial tubes (*a*, *fig.* 211.) end. The latter are convective channels, and fulfil only a mechanical purpose; the former is the immediate seat of the respiratory process. These two parts differ no less in anatomical structure than in mechanical conformation. The bronchi terminate in the "intralobular bronchial ramifications" (Addison); "lobular passages" (Todd); "intercellular 'passages" (Rainey); "mouths of the infundibula" (Rossignol). These are different designations only for one and the same thing. The passages in which the bronchi end are greater in diameter than the bronchi themselves. Their sides are at first *smooth* (*a*), like those of the bronchial tubes; they become afterwards loculated (*c*) with cells or alveoli, like the terminal air-cells (*e*, *b*) (*vesiculæ* s. *cellulæ aëreæ* s. *Malpighianæ*, *alveoli pulmonum* Rossignol. *Luftzellen oder Lungenbläschen* of the German writers). *Looking down* along a section through one of these passages, it is perfectly easy to define either an "infundibulum," or a broad-based passage bounded by *Malpighian* cells. It is, however, perfectly certain that Rossignol has given in his illustrations far more regularity of outline to these

Fig. 212.



(*After Harting.*)

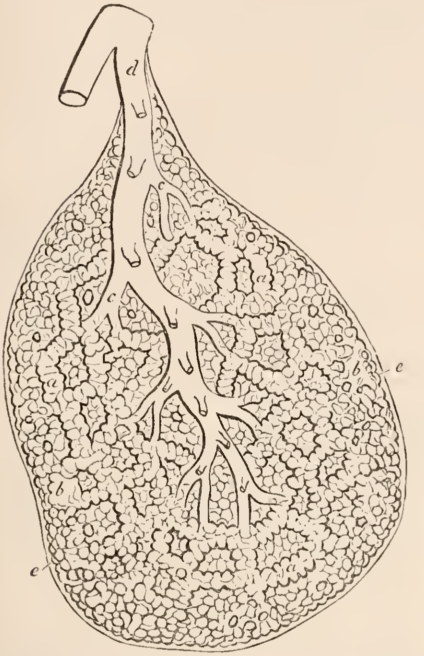
a is the termination of a bronchial tube properly so called, ending abruptly in an intercellular passage marked by its cellulated parietes. *b*, *e*, cell-tissue.

parts than they present in the actual preparation. The intercellular passages (Rainey), then, are those *continuous* channels in the lobule which are laterally sacculated by cells. They conduct the air to and from every part of the lobule. They give rise to secondary passages (*b*, *e*, *fig.* 208.), which again lead to a third, &c., all communicating with a group of air-cells. Each of these passages with its appended system of cells, if bounded by an *imaginary* outline, *may* certainly be called an "infundibulum." The intercellular passages *unite* and *divide* (*a*, *fig.* 210.). They thus intercommunicate. In this particular they are distinguished from the bronchial tubes (*b*, *fig.* 210.; *c*, *fig.* 212.), which never inosculate. The latter are merely convective passages; the former are expressly organised for the office of respiration. The bronchi diminish in calibre as they divide; the intercellular passages rather enlarge in diameter (*f*, *fig.* 213.). The former preserve in their branchings one main direction; the latter run through the lobule at every angle. They are perforated at every point by secondary passages (*a*, *b*, *e*, *fig.* 212.) of varying lengths and directions: sometimes only by a deeper cell than ordinary. M. Bourgery saw in this arrangement only a "labyrinth of canals" (*canaux ramifiés bronchiques.*) Home and Bauer, mistaking the intercellular passages for the bronchi, remark, "the cells of the human lungs are not dilatations of the bronchial tubes, but are regular cells in which the

* Mikroscopisch-Anatomie, Sweiterbund, Leipsic, 1850, and Handbuch der Gewebelehre des Menschen, von Kölliker, Leipsic, 1852.

tubes terminate." This really coincides with the supposition of Reisseissen: — "tracheæ ramos ita per pulmones distribui, ut facta partitione multiplici, singuli quique cœcis nec ampliatis terminentur finibus, quibus vesiculæ aëriferæ constituantur." Moleschott has slightly modified the views of Reisseissen: — "Jam singulos ductus aeriferos, non uti

Fig. 213.



An imaginary section of a lobule of the human lung, carried parallel with the plane of distribution of the chief interlobular divisions of the bronchi. The latter are observed to multiply both on the dichotomous and arborescent plan. (*Original.*)

c, c, denote the smallest of the true bronchi which contrast by their smooth walls the alveolated intercellular passages *a, a, a*. The latter exceed the extreme bronchules slightly in diameter. Unlike these bronchules (*c*), which never inosculate, the intercellular passages (*a*), ramify in every direction and at every plane, and frequently open into one another, establishing thus a free communication for the air between all parts of the lobule. *b, b, b*, indicate the ultimate air-cells of the lungs. They correspond in size with the alveoli (themselves true cells) on the walls of the intercellular passages. *e, e*, bottom of the sub-pleural or most superficial air-cells.

Reisseissen voluit, cœcis nec ampliatis finibus terminari dicit, verum ad latera parietalibus vesiculis instructos esse testatur." Kölliker adopts the views of Rossignol, and constructs an illustration which expresses more perfectly the views of the latter author. *

If a series of hollow cells were disposed linearly, the points of contact being converted into foramina, as represented in this diagram, they would accurately answer to the description of the "intercellular passages" (*'a'*, *fig.* 210.; *'a'*, *fig.* 212.). It is, therefore, obvious that two different minds, contemplating the same

Fig. 214.

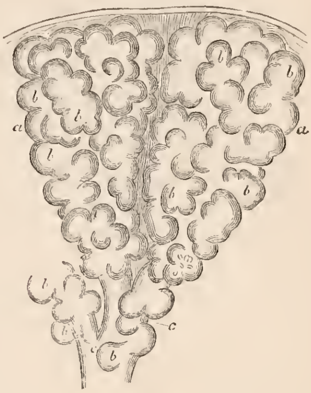


Diagram of two lobules a, a, *of the human lung.* (*After Kölliker.*)

b, b, b, b, ultimate air-cells; *c, c*, the finest bronchial tubes. (Magnified 25 diameters.)

objects under two different preconceptions, would see in them "passages" or "*infundibula*." A lung injected with wax readily misleads to the

Fig. 215.

(*After Rossignol.*)

b, extreme bronchial tube of the human lung terminating in the "infundibula;" *a, a*, infundibula multiplied into cells on their parietes.

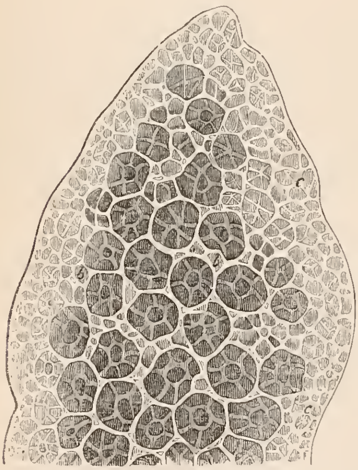
error committed by Reisseissen of supposing each cell to be the separate termination of a separate bronchial branch. But it is certain

* "Mit denselben stehen dann die letzen Elemente der Luftwege, die Luftzellen oder Lungen bläschen, in Verbindung, doch nicht so, wie man früher glaubte, dass jedes feinste Bronchialästchen *terminal* in ein einziges Bläschen ausgeht, sondern in dem dieselben immer mit einer ganzen Gruppe von Bläschen sich vereinen. Diese Bläschengruppen entsprechen den kleinsten Läppchen traubenförmiger Drüsen, und es ist daher nicht die geringste Nöthigung vorhanden, dieselben mit einem andern Namen zu bezeichnen, wie *Rossignol* der sie *infundibula* nennt, wenn auch zuzugeben ist, dass ihr Bau in manchen eigenthümlich sich verhält. Während namlich in andern Drüsen die Drüsenbläschen, wenn sie auch nicht so isolirt für sich bestehen, wie man bisher angenommen hat, doch eine gewisse Selbständigheit haben sind, die ihnen entsprechen Elemente in den Lungen, die Luftzellen, in bedeuten Grade untereinander verschmolzen, so dass alle einem Läppchen angehörigen Bläschen nicht in Abzweigungen der zu demselben tretenden feinsten Bronchialästchen, sondern in einem gemeinsamen Hohlraum einmünden aus dem dann erst das Luftgefäss sich entwickelt." —Mic. Anat., Zweiten Hälfe, p. 309.

that Reisseissen mistook the *infundibula* of Rossignol which are loculated with the ultimate cells, both terminally and laterally, for the separate ends of separate bronchial tubes. It is no less certain that Rossignol has disposed with unnatural precision the "cells" and "passages" of which the lobule is composed. Schultz, again, has erred in viewing the intercellular passages in the light of "bronchial petioles:"—Bronchiolorum continuationes ita constructas causis supra dictis commotus appellaverim petiolos, atque hanc denominationem novam commendo, fines autem eorum amplificatos nomine jam antea ipsis indito infundibula voco; eos denique alveolos, qui in petiolis reperiuntur alveolos parietales, omnes vero, qui in infundibulis occurrunt, alveolos terminales nomino."*

Professors Schröder Van der Kolk, Harting, Promotor, and their pupil Adrius Adriani, adopt the opinions of Rossignöl in relation to the disposition of the air-cells and passages within the lobuli. Whether the intercellular passages be distinguished by that name or by that of the *infundibula*, it is certain that they differ both from bronchial tubes and from the ultimate air-cells by *a greater diameter*. The nearer they are to the point of their attachment to the bronchial tubes, the more tubular or cylindrical their figure or outline; the further, the more irregular and inosculating, until

Fig. 216.



A section at right angle to the axes of the "infundibula," showing the alveoli (b, c). (*After Rossignol.*)

finally they terminate in air-cells; not after the manner supposed by Reisseissen in form of a Florence flask; for the extreme cell has the same diameter as the tube itself. From the accompanying diagram, constructed by the author, the relation between the bronchi, intercellular passages, and air-cells will be readily understood.

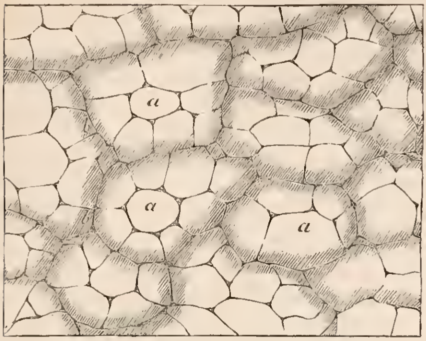
It is, then, important to remember that the intercellular passages are open spaces between the ultimate cells, their walls being constituted of these latter. Like the ultimate cells, therefore, they participate *actively* in the process of respiration. They are not *merely* convective conduits. Since they proceed at every plane and angle from the centre of the lobule, a section of the latter in *any* direction will cut these passages both transversely and longitudinally.

Ultimate Air-Cells of the Lungs.—Vesiculæ, s. cellulæ aëreæ, s. Malpighianæ, alveoli pulmonum; Rossignol.—An air-cell in the human and mammalian lung is a space circumscribed by a single wall of reticulated capillaries, and varying infinitely in figure, and presenting in different parts of the lung numerous varieties of size; each cell having *an opening* embracing a section, more or less considerable, of its circumference. The cells on the walls of the intercellular passages (the sides of the infundibulum of Rossignol) may be defined as mere cup-shaped depressions, sometimes perforated at the bottom by a large foramen opening into one or more cells. Under the pleura the air-cell occurs as a four or six-sided chamber, of which the bottom, presenting under the pleural membrane, is rounded, and might readily be mistaken for the fundus of a pear-shaped vesicle, the apex running into a bronchial tubule. If a cell, situated in the central parts of a lobule, be selected for examination, it will be found as a polyhëdral alveolus, one or two or more of whose sides are deficient or converted into a *foramina*, through which its enclosed space communicates with those of contiguous cells. No cell is a perfect geometrical figure—such, that is, as would be formed by regular plane sides; because ridges and partial partitions, from the encroachment of the angles of neighbouring cells, project into and multiply its interior. It is not often that the eye falls upon a unilocular cell having only one opening: they occur most frequently as irregular, angular spaces, with one or more imperfect sides, *fig.* 219. Those cells which communicate directly with the bronchial tubes and intercellular passages open into them by large circular apertures; and they are themselves similarly perforated, to communicate with other vesicles, which again open into others beyond them; so that each of the openings in the air-passage leads to a *series* of cells, extending from it to the surface of the lobule. The vesicles which communicate directly with the air-passages are more minute, and have a closer vascular network than those which lie nearer to the surface of the lobule; an arrangement which is in beautiful harmony with the relative facility by which the air in them respectively is renovated. The diameter of the human air-cells is about twenty times greater than that of the capillaries which are distributed upon their parietes, varying, according to the measurement of

* Disq. de Struc. et Text. Canal. aërif. Scripsit Ernest Schultz, Lypsiæ, 1850, p. 34.

Weber, from the $\frac{1}{200}$ to the $\frac{1}{70}$ of an inch. It has been calculated by M. Rochoux that

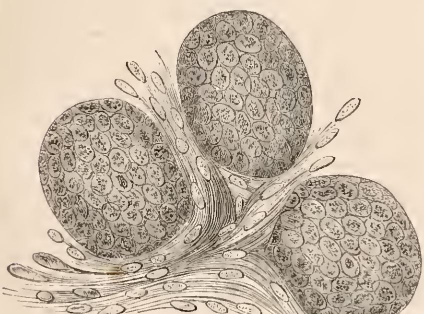
Fig. 217.



Pleural surface of the human lung, indicating the lobules in shaded outline, and the air-cells a, a. (*After Adriani.*)

as many as 17,790 air-cells are grouped round each terminal bronchus; and that their total number in the lungs amounts to no less than *six millions*. The dimensions of the air-cells given by M. Moleschot*, are very much less than those of Rainey and Kölliker. According to the former observer, they range from $\frac{1}{120}$th to $\frac{1}{1200}$th of an inch: those of Carpenter and Kölliker correspond with those of Weber already stated. They continue to increase in size from birth to old age, and present in man a greater capacity than in woman. Dr. W. Addison supposed that the air-cells did not exist *before* birth, that they were mechanically formed by the first act of inspiration, and that the foramina between the cells were really ruptured partitions caused by the pressure of the atmosphere.

Fig. 218.



Ultimate pulmonary tissue from a fœtus three months old. (*After Harting, quoted by Adriani.*)

a, a, a, primitive "infundibula," of which the parietes are as yet composed only of minute oval cells (*c*); *b, b, b,* elastic tissue occupying the intervals between the infundibula, exhibiting the nuclei of its cells.

* Op. cit.

It was, however, first proved by Mr. Rainey, and by Professor Harting more lately, that they exist nearly as perfect in contour before as after birth. Neither the form, the number, nor the disposition of the air-passages and cells can any longer be held as the offspring of chance, but as the nicely adjusted products of marvellous foresight and design.

The preceding statement will enable the reader to understand the sources of the differences by which the views of different writers upon the structure of the lungs are marked. It is easy to make a "labyrinth," a "passage," or a "group of vesicles," or "a funnel-shaped arrangement of cells," out of the complex appearance which a section of an inflated and dried lung presents. It is important to observe that the classification of the cells into the *parietal* and *terminal*, as suggested by Rossignol, is calculated to lead to a false idea as to the real arrangement of the air-cells within the lobule. The capsule of the *lobule* encloses a pear-shaped space; but this is not the infundibulum of Rossignol. This ingenious author applies this term to those parts which Mr. Rainey and Dr. W. Addison have distinguished as the air-passages surrounded and terminated by secondary passages and air-cells. The *septa* bearing *alveoli* which project everywhere into the funnel of Rossignol, render the word *parietal*, as applied to them, altogether unmeaning. Every recent observer admits that the air-cells open everywhere into one another, such that the air entering one intercellular passage at one part of the lobule would traverse its entire extent through the intervening labyrinth of cells, and return through another air-passage into the same peduncular bronchus.

When *two sides* of two contiguous air-passages or cells come into opposition, the resulting partition is not composed of *two* layers, but *one*. If the cells were *formed* by the protrusive force of the air in entering in the first act of inspiration, such partitions would, of mechanical necessity, consist of *two* layers: they are, however, formed by an act of *organisation*. This curious and distinctive fact in the history of the human and the mammal lung will be again referred to. As the partitions of the cells are organised *before* birth, it follows that the geometrical outline of each cell must be determined before the first act of inspiration. The same argument applies to the *foramina* between the cells. They are not accidental perforations; they are definitively and designedly organised orifices, and are sustained in a permanently patulous state by an arch-like arrangement of elastic fibres, which will be afterwards described.

As the air-cells of the lungs of mammals generally bear no proportion in size to that of the body of the animal, so in the human subject there is no relation between the dimensions of these cells and the stature of the body; and it is probable that no estimate can be formed of the vital capacity of the lungs from a calculation of the individual dimensions of the air-cells. It should be observed that the orifices, by which one cell communicates with another, are of the same shape and dimensions as those which exist between the first set of cells and the bronchial tubes; they can be very distinctly seen by looking down upon the air-cells from the intercellular passages, focussing the microscope at the same time. Since these openings are not necessarily in a straight line, the exact number of cells which communicate cannot in this manner be determined; but the number will depend upon the distance which intervenes between any given part of the bronchial passage and the surface of the lobule: so that when a bronchial passage arrives nearest the surface it will be separated from it only by a single terminal cell. The dimensions of the cells in different animals present many diversities. In the lung of the kangaroo, especially in those parts remote from the surface, the air-cells are very small, and disposed with the greatest irregularity. The lining membrane is also proportionally imperfect, being perforated in many places opposite the areolæ of the plexuses, so as to admit the air passing through them to come into contact with the coats of the vessels, as in the lung of the bird. In this mammal the minuteness of the air-cell is such, that it is too small to contain a *single ciliated* epithelium (*Rainey*). In the lung of the rat and mouse the air-cells are still more minute, and certainly many of them are not of a sufficient size to receive even an individual particle of the dimensions of the bronchial ciliated epithelium. The air-cells are disposed with the same kind of irregularity, and the pulmonary membrane is deficient, as in the lung of the kangaroo. In the lung of the hare, the air-cells are very small, but perhaps not so much so as in the preceding species. The lung of the rabbit resembles that of the hare, but its air-cells are rather larger. In the lung of the dog the air-cells are larger than in the rabbit; but still in the more central parts of the lung they are very minute, too minute, indeed, to be capable of having a lining of *ciliated* epithelium without being wholly unfitted for the purposes of respiration. In the monkey, the air-cells are large, and resemble those in the human lung. In the lung of the sheep and ox they are, upon the whole, about the same size, and very minute in both.*

The diameter of one of the intercellular passages ranges from $\frac{1}{100}$ to $\frac{1}{200}$ of an inch, and that of the cells from $\frac{1}{200}$ to $\frac{1}{300}$ (*Todd* and *Bowman*). In the lung of the calf these cells do not exceed $\frac{1}{600}$ By Dr. W. Addison they are stated, in the human lung, to measure from $\frac{1}{200}$ to $\frac{1}{500}$ of an inch.

Minute Structure of the Air-Cells. — Three anatomical elements enter into the composition of the air-cells: the epithelium, the blood-plexus, and the elastic tissue. The interlobular tissue is not here considered.

1st. *The Epithelium of the Air-Passages and Cells.* — It was first surmised by Dr. Thomas Addison, from the phenomena of the difference between pneumonia and bronchitis, that the air-cells of the lungs must be destitute of epithelium. Dr. W. Addison contends that the air-cells "possess an epithelium in form of large round nucleated scales, and from one to fifteen or more nuclei may be counted in a single scale. A great many nuclei without any epithelial envelope may be seen upon them; but I have never satisfied myself that they possess the ciliated cylinder epithelium so abundant in the trachea and bronchi."*

Mr. Rainey denies the presence of epithelium of *any description* on the interior of the air-cells, the vascular plexus being *lined* only by a "pulmonary membrane." Rossignol is the only subsequent writer who has supported this view: — "Neither does the ciliated epithelium lining the bronchial tubes extend into the intercellular passages, and from thence into the air-cells, or rather air-spaces (speaking of the bird's lung), but it ceases where the bronchial membrane terminates. In the mammal, but especially in man, in whom the air-cells are very large, *the fact of their having no epithelial lining* can only be proved by a careful examination of the parts with the microscope, and therefore, with no other means than those of deciding this question, it might always remain *sub judice*, so long as persons are found who are more ready to confide in the assertions of others than submit to the pains and difficulty of examining the point for themselves."† Rossignol says: "Les parois alvéolaires sont formées: 1° par une charpente de fibres qui laissent entre elles des espaces vides ou aréoles; 2° par *une membrane transparente*, qui n'offre aucune trace de fibres, qui recouvre la charpente précédente, et remplit les espaces vides." In this passage M. Rossignol has evidently adopted without inquiry the conclusion of Mr. Rainey, with whose writings he seems well acquainted. The opinion of all German and English anatomists is now finally formed with reference to this

* As the following passage expresses the views of S. van der Kolk, Harting, Kölliker, as well as that of the writer, Adriani, I append it here at length: —

"Has cavitates antea cellulas dictas, nunc Dr. Rossignol alveolos nuncupavit, quod admitti potest, si nemo tantum huic nomini regularitatem mathematicam adjungat, quæ in alveolario apium invenitur; in pluribus locis enim alveoli infundibulorum aut rotundi sunt, aut magis polygonam figuram referunt; eorum parietes vasis cinguntur minutissimis, confertissimis, sæpe optimè materia colorata impletis, et tunc rete subtilissimum constituentibus. Fibræ autem elasticæ potissimum ad margines septorum, quibus alveoli constituuntur, decurrunt, tamen uti jam monuimus, nonnullæ per parietes ipsos etiam decurrunt. Vasa capillaria majora hac tela sustinentur. In ipsis parietibus infundibulorum alveoli inveniuntur, in ipsos bronchiolorum ramos sese ostendentes; Rossignol, qui etiam illos vidit, eos alveolos parietales vocavit; nos autem, antequam ejus commentatio fuerat edita, *cellulas* parietales vocavimus."—P. 43. Op. cit.

* Phil. Trans. 1842, part i. p. 162.

† Rainey, Med. Chir. Trans. vol. xxxii. 1849.

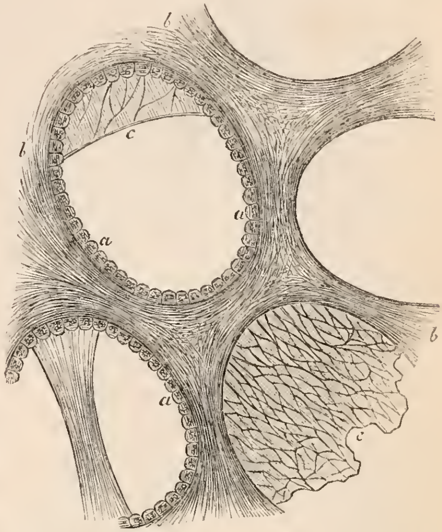
point. Carpenter, Quain and Sharpey, Kirkes and Paget, Kölliker, S. Van der Kolk, Harting, Adriani, and Schultz *describe a pavement epithelium on the interior of the air-cells of the lungs;* and the author who has devoted many special examinations to this particular point is now convinced that a fine pavement epithelium *does* cover these parts which he proposes to distinguish as the "*hyaline epithelium.*"* Messrs. Todd and Bowman, like Rossignol, adopt the views of Mr. Rainey, and teach that the air-cells have no epithelium of *any kind.* The adjoined is the illustration of the epithelium given by Schroeder Van der Kolk in Adriani's Essay.†

Fig. 219.

Ultimate cells of the human lung, showing the trabicular framework formed by the elastic fibres of the walls, and the hyaline pavement epithelium which lines the interior of the air-cells. (After Schroeder Van der Kolk, quoted by Adriani.)

By this distinguished observer it is represented under the character of transparent pavement epithelium, the cells of which are furnished with a nucleus and *minute* granules They are adjusted accurately, as a single layer, edge to edge. The description given by Kölliker coincides with the preceding.*

Fig. 220.



A thin section of a few air-cells from the human lung, viewed by transmitted light. (After Kölliker.)

a, epithelium lining the air-cells; *b*, elastic tissue arching over and between the cells; *c*, the flat wall of a cell, showing the scanty distribution of elastic fibres over this part of the cell.

By Kölliker the cells of this epithelium (*a*, *fig.* 220.) are stated to consist of polygonal particles of from 1—1600th to 1—2250th of an inch in diameter, and from 1—2800th to 1—3800th of an inch in thickness. They repose immediately upon the fibrous layer. They are normally *shed;* though not readily detected in health, it is easy to discover these epithelia in disease. This epithelium lines every part of the air-passages and cells *except* the bronchi. These latter tubes are furnished with a thick layer of *ciliated* epithelium, which, as formerly stated, terminates abruptly at the commencement of the intercellular passages. It may

* In suggesting the word *hyaline* as a distinctive epithet for this variety of epithelium, I do not wish to be understood as denying, in its component scales, the existence of every form of visible element. The word should be accepted in a comparative sense, as signifying that their nuclei and granules are less declared than those of any other description of epithelium.

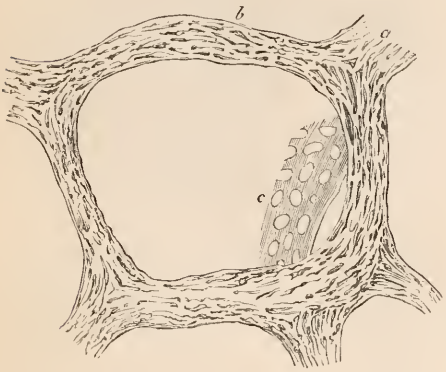
† This figure is thus described by Adriani:— "Alveoli constant membrana subtilissima structura carente, quæ autem membrana mucosa tegitur epithelio pavimentoso (*plaat epithelium*) admodum pellucido, in quo potissimum ope acidi acetici nuclei conspiciuntur; propter singularem autem pelluciditatem sæpe difficile est, illud epithelium rite distinguere; vid. fig. 12. nostram, ubi ad alveolorum parietes conspicitur. Cellulæ conicæ ciliatæ quæ in bronchiolis minutis adhuc conspiciuntur, in alveolis penitus deficiunt; hæc membrana cum epithelio pavimentoso obtegit vasa sanguifera per alveolorum parietes ducta; propter singularem tenuitatem imbibitio atque absorptio per hanc membranulam facillime perfici posse facile intelligitur."—Op. cit. p. 61.

* The following passage in the Microscopic Anatomy of Kölliker refers to the figure cited in the text. "Das Epithelium der Lungenbläschen ist kein flimmerndes, wie man früher ziemlich allgemeine annahm, sondern ein gewöhnliches Pflasterepithelium, das mit polygonalem Zellen von 0·005—0·007‴ Durchmesser und 0·003—0·004‴ Dicke in einfacher Lage unmittelbar auf der Faserhaut der Luftbläschen aufsitzt. Die Zellen sind alle kernhaltig, und haben meist ausserdem der *Trachea* und der Bronchien anzunehmen, dagegen können allerdings mehr zufällig oder dann in Krankheiten der Luftwege einzelne Elemente desselben dem Bronchialschleime sich beimengen. Beim Menschen fallen diese Zellen ungemein leicht ab und liegen dan frei in den Luftbläschen und feinsten Bronchien, doch kann man fast in jeder Lunge, wenigstens in einzelnen Alveolen dieselben noch *in situ* sehen und bei eben getödteten Thieren bietet bei Beobachtung der Lagerung derselben nicht die geringsten Schwierigkeiten dar."—Op. cit., p. 315.

then be accepted as a fixed conclusion in the histology of the lungs that the air-cells are lined internally by a single layer of "*hyaline epithelium*." This conclusion is corroborated by the minute structure of the respiratory organs in *all animals*. In *none* are the vessels absolutely naked.

Elastic Tissue of the Air-Cells.—The existence of this tissue is admitted by every anatomist who has studied the subject. Its disposition amid the air-cells is less known. It fulfils a part, though mechanical, of the highest consequence to the movement of the lungs in respiration. The fibres of this tissue belong to the yellow variety. They resist both the action of acetic acid and liquor potassæ. They are most visible in the lungs of the cetacei. They are readily detected in those of all mammals.

Fig. 221.



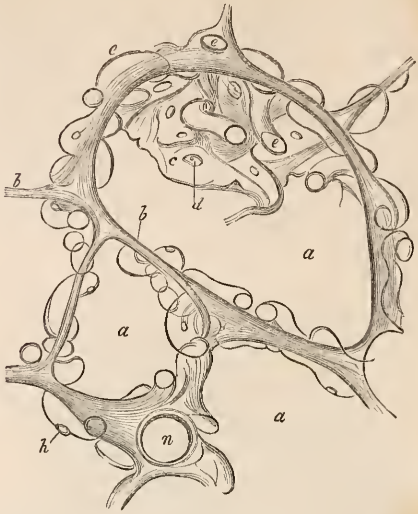
(*After S. Van der Kolk.*)

a, *b*, elastic tissue (with thick yellow fibres) bounding an air-cell in the lung of the whale; *c*, a small portion of the wall of the same, showing the capillary web injected.

They are limited chiefly, in distribution, to the edges and margins of cells. They encircle foramina, and maintain them by their elasticity, in a patulous state. They not unfrequently arch over the roof of the air-cells, constituting to the latter true *trabeculæ*. They pass from cell to cell, and form an important connecting tissue. They are everywhere arranged in bands or fascicles, or in a large meshed network of single fibres, as shown in the adjoined figure.

When they are distributed over the flat surface of an air-cell, they are situated immediately under the epithelium. As there are two epithelial surfaces to each cell-wall, the intermediate vascular plexus being single, it follows that the elastic fibres must run over and between this plexus on both of its surfaces. A real framework is thus constructed which is well adapted to support the capillary layer; and this is an important function, which devolves on the elastic tissue. The framework formed by this tissue over the walls of the air-cells is so large-meshed that it does not obstruct the contact between the air and the blood. These two elements are separated only by a slender hyaline lamina

Fig. 222.



View of a thin section of the lung of a Cat, which had been injected by the pulmonary artery with gelatine, so as to fill blood-vessels and air-cells, and had been sliced when cold. (After Todd and Bowman.)

a, *a*, *a*, air-cells and lobular passage in section; *b*, *b*, their fibrous wall in section; *c*, their wall in face; *d*, extremely faint nucleus in the same; *e*, *e*, capillaries; *h*, nucleus in wall of capillary; *n*, small pulmonary artery, or vein with simple wall. (Magnified 250 diameters.)

of epithelium and the coats of the blood-vessels. At the edges, angles, margins of cells and the foramina between the latter, the fibres of this tissue are gathered into dense and strong bands having an arched and circular disposition. It is suspected by Kölliker that there may be muscular fibre-cells among this tissue in the air-cells, like those already described in the walls of the bronchial tubes. But the long nuclei which occur in the walls of the air-cells, seen also by Mr. Rainey and frequently by the author, are situated in *the substance* of the tunics of capillary blood-vessels. They are neither so large nor so long as the unstriped muscle *nucleus*. In the walls of the bronchi the elastic fibres were described as denser and stronger than those of the walls of the air-cells, and as observing almost exclusively a longitudinal arrangement, the muscular fibres being disposed circularly. Among the air-cells they exhibit that order and plan which fit them best to subserve the mechanical exigencies of the part. Harting, S. Van der Kolk, and Promotor have detected these fibres in the sputum of phthisis, which they regard as characteristic of the existence of a vomica. A failure in the mechanical property (elasticity) of this tissue amid the air-cells is probably one of the conditions of emphysema.

Vascular System of the Lungs.—The blood-system of the lungs constitutes a separate system: "the second, pulmonary, or small circulation." The nutrition of some parts of these organs is sustained by another order of vessels, distinct from these.

The *pulmonary artery*, conducting venous blood, and proceeding from the right ventricle, is the channel by which the blood destined to be arterialised is conveyed to the lungs. It is circumscribed in its distribution to the area of the true pulmonary tissue as distinguished from the bronchial. The plexus formed by its branches is emphatically the *rete mirabile*. The branches of the pulmonary artery follow those of the bronchi as far as the origin of the intercellular passages; a point at which they assume an irregular course over and between the cells. A lobule of the lung receives, with great regularity, only a *single* ramusculus from the pulmonary artery. It is not so large in size as the bronchial tube which it accompanies. Within the lobule, the artery coincides with the tube in its divisions, which are here more intimately bound together than at the extralobular stages of their course. It was supposed by Bourgery that the artery formed a framework of vessels around the tube. This is not the case. Of course, many of the branches of the pulmonary artery course between the lobules in order to reach others more distantly situated. Reisseissen conceived that he had traced a ramuscule of the pulmonary artery to the root of each "vesicle," describing a venule on the other side. Krause supposed that each individual cell, with unvarying constancy, had its artery and vein, and intermediate plexus.* Berres believed that each cellule presented, on its circumference, a great many facets, like the eyes of insects, each facet having its own plexus. Rossignol † embraces the views of Krause which assign a separate arteriole and venule to each cell. In the accompanying figure, taken from the essay of Adriani, and drawn from a preparation by Schroeder van der Kolk himself, the branches of the pulmonary artery are seen to run, not only between the ultimate air-cells, but in many instances through the very centre of the walls.

With this view the exact description of Mr. Rainey coincides:—"In the mammal the number of capillary plexuses is not, as some have supposed, the same as that of the air-cells; that is to say, a terminal artery does not divide into a plexus at any particular part of a cell, its branches uniting for the commencement of a vein on the opposite part. On the contrary, one plexus passes between and supplies several cells. In the interior of the lung the exact extent of an individual plexus cannot be determined, in consequence of the removal of some part of it by the section necessary for its exhibition. But, on the surface of the lung, where the extent of these plexuses, in relation to the cells over which they ramify, can be easily made out, an individual plexus may be seen to spread over an area of ten or twelve cells in some parts and in fewer on others, the exact num-

Fig. 223.

A thin slice (near the pleural surface) of the lung of the Cow, with the pulmonary artery (a), *and pulmonary vein* (c), *injected.* (*After Schroeder Van der Kolk.*)

a, large arterial trunk terminating abruptly in small branches (*b*, *b*, *b*), which travel between and along the borders of the air-cells, and in the ultimate capillaries *e*, *e*, by short trunks as shown at *d*; *f*, *f*, foramina arising from the sections of intercellular passages; *g*, fibrous trabeculæ, supporting by their elasticity the cells, and preserving their wall at a regulated tension.

ber depending in some measure upon the size of the cells." *

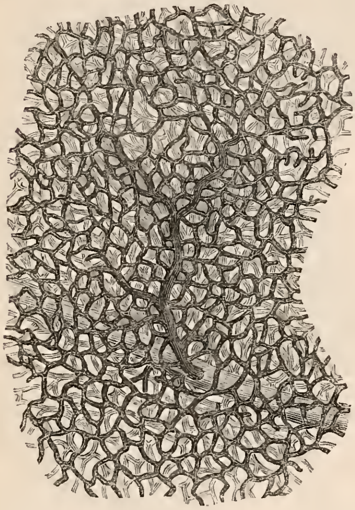
Around the foramina and margins of the cells very frequent anastomosis takes place between the minute branches of the pulmonary artery. With reference to this artery, it should, however, be stated, that it differs from all other arteries in the extremely *infrequent inosculations* which occur between its secondary and tertiary branches—and that its blood mingles with that of no other vessel; it is poured entire into the pulmonary veins. "The trunk" of a vessel is most certainly very seldom seen

* Huschke, Encycl. Anat. Splanchnologie, p. 233.
† Op. cit. p. 56.

* Op. cit. p. 7.

on the flat expansion of a cell-wall. But it is quite an error to suppose that each cellule has its own separate arterial ramuscule. Professors Harting and S. Van der Kolk's injections place this point beyond doubt: — "quod ad divisionem ramorum arteriarum attinet, animadvertendum est, non alveolum quemque singulum ramulum accipere, quum hoc tantum valeat de infundibulis, ita ut lobulus, infundibula continens, accipiat truncum arteriæ, ille truncus ad numerum infundibulorum dividatur et iterum subdividatur." (Adriani). From this description it results that the capillary *web* without an intervening trunk stretches from cell to cell. One more important fact remains to be stated with reference to the capillary plexus. *It is nowhere doubled upon itself,* as it is in the lung of the reptile. Every cell-wall and every partition between the cells bears only a *single* layer of vessels. The opposed sides of such a layer must therefore bound two different cells, and the current of blood by which it is traversed must be subjected on *both* its flat sides to the action of air contained in the cells. If this plexus were double, only *one* side could receive the influence of the atmosphere. *This* type is exemplified in the reptilian lung. All other things being equal the respiration of the mammal and man must be twice in amount that of the reptile. But this anatomical fact has also an interesting pathological bearing. When the capillary layer, or rather the blood borne by it, is the seat of disease, the products of that disease must be poured into the two contiguous cells, between which it is interposed, at the same time and in the same amount. This accounts for the rapidity with which pneumonic infiltration occurs. In the most injected preparation the diameter of the capillary vessels of the *rete mirabile* exceeds that of the meshes. This, however, is not an exact expression of their proportions in the living state. The diameter of a single capillary, measured in the injected state on the wall of an air-cell, does not exceed $\frac{1}{1800}$ (Todd and Bowman.) The human red blood corpuscle ranges, in the same drop of blood, from $\frac{1}{4000}$ to $\frac{1}{2800}$ of an inch in diameter, the average being from $\frac{1}{3500}$ to $\frac{1}{3200}$. Then *two* red-corpuscles may traverse any single capillary abreast? When allowance is made for the difference between the internal and external diameters of the vessel, it will appear very probable that in man and mammals only a *single* row of red-corpuscles traverse the pulmonary capillaries at a time. In the lung of the reptile it is to be proved by observation of the living circulation, that a double row of corpuscles really does move along the vessels. This fact must reduce the amount of oxygenation which in a given time a single corpuscle receives.

Fig. 224.



Injected preparation of a single arterial twig and the attendant vein, showing a single plane *of capillaries overlying the air-cells. The pleural capillary system is distinguished from that of the true pulmonary tissue by the greater denseness of the vascular web and greater minuteness of the meshes in the latter situation.* (*After Kolliker.*)

The *pulmonary Veins* convey the blood, arterialised in the plexus just described, to the left auricle. The distribution of the pulmonary veins differs strikingly from that of the artery and bronchia. Each lobule has its separate arterial and bronchial branch. This regularity does not obtain with respect to the veins. The pulmonary veins arise in the form of minute radicles in the capillary plexus of the air-cells. Now although, as formerly stated, the individual air-cells are not furnished with a separate arteriole and venule, the extreme branches of the pulmonary artery and the incipient venules are separated in different parts of the lung by *areas* of similar dimensions. It follows, therefore, that the *time* during which a globule of blood in different parts of the lung is exposed to the agency of the air is equal; in other words, every drop of blood which enters the lung is arterialised to the *same* amount from the equality of the areas of exposure over which it passes. It should also be observed that as the capillary web is spread over *several* cells, every particle of blood *in transitu* from artery to vein traverses the circumferences of *several* cells. This is a beautiful provision for securing *certainty* to a vital process. The minute venules unite to form visible trunks, which course irregularly over and between the cells and intercellular passages. They observe a general diagonal direction, the bronchia and artery occupying with great constancy the geometrical axes of the lobule. They emerge out of this lobular space not at its apex, in company with the air-tube and artery, but at every or any point of its circumference. This is more obviously the case as regards the lobular veins along the surface of the lung. Those more centrally situated follow the bronchia more closely. This explains why Reisseissen, Cruveilhier, and others have expressed very opposite opinions upon this point. In the intralobular spaces the veins proceeding from several lobules unite together into a trunk common to them all. The larger trunks, resulting from the confluence of the smaller, converge towards the roots of the lungs, but by a route different from that of the bronchia and arteries. Thus the general mass of the lung may be regarded as containing two series of ramified canals; one transmitting the bronchial tubes, the nerves and pulmonary artery, the other the pulmonary veins. This interesting fact was well described by Dr. Addison of Guy's Hospital in a paper in the Medico Chirurgical Transactions in 1840. At the root of the lungs four pulmonary veins result, which discharge their blood into the left auricle. "The cause of the separate course of the pulmonary arteries and veins is to be found in the opposite position of their radicles in regard to the capillary net-work of the lobules, it being a convenient arrangement for the terminal arterial and venous twigs to hold alternate positions among the capillary net-work, so that each arterial twig dispenses its blood in all directions, and each venous radicle collects it from all sides." *

The Bronchial System of Vessels consists of arteries and veins. The bronchial arteries are commonly described as the nutrient vessels of the bronchial tubes. They arise from the front of the descending or thoracic aorta. They are, however, variable in number as well as in place of origin. They are commonly described as the inferior and superior.

The *superior*, two usually in number, arise either separately or by a common trunk from the front of the aorta, opposite the third or the fourth dorsal vertebra, and one directed to each side adheres to the posterior surface of the bronchial tube, on which it divides into branches, and passes into the interior of the lung.

The *inferior*, two or more in number, arise lower down than the preceding, and are distributed, like them, on the bronchus of each lung: these small arteries give branches to the œsophagus, bronchial glands and pericardium. The superior bronchial artery of the left side may arise from the superior intercostal artery. Every successful injection exhibits large and long branches from these vessels, leaving the tracks of the bronchi, and entering into the inter-lobular tissue and sub-pleural tissue. †

The *bronchial Veins* accompany the arteries, and the branches unite one for each side; the right opens into the azygos vein, and the left into the superior intercostal vein. Many branches may be traced also to the œsophageal veins, and those of the posterior mediastinum. Numerous branches of these veins may be observed to wander under the pleura, in the sub-pleural tissue.

Anastomoses between the Bronchial and Pulmonary Systems of Vessels. — Since the days of Ruysch, Haller, Soemmering, and Reisseissen, this has proved a vexed question in anatomy. One point in this controversy has been overlooked. The bronchial arteries are said to be the nutrient vessels, not of the *lungs*, but of the *bronchi.* The tissue composing the structure of the air-cells and intercellular passages of the lungs is nourished by the blood of the *pulmonary* system. In the lungs of Reptiles there exists no bronchial system of vessels. The solid walls of these organs are occupied exclusively by the *pulmonary* system. It is upon the latter, therefore, that the function of *nourishing* the substance, the *parenchyma*, of these organs *must* devolve in these animals. Thus is proved the *capacity* of this blood. The epithelial particles and elastic fibres of the air-cells derive the materials of their nutrition from the blood of the plexus (the true pulmonary) on which they immediately lie. It is indisputable, therefore, that the afferent blood of the lungs, like that of every other gland, discharges a twofold office,—that proper to the gland, and that of nourishing its tissue. *Two systems* or layers of capillary plexuses are discoverable on the walls of the bronchial tubes; one lies immediately underneath the mucous membrane, and exhibits extended oblong meshes, which run parallel with the yellow elastic fibres; the other lies on the *outside* of the circular muscular layer, so that the stratum of muscles is interposed between the two systems of vessels. This outer layer of vessels, its trunks and capillaries, run circularly with the fibres of the muscles and at right angles with those of the submucous layer. The blood of the former empties itself into the pulmonary vessels; that of the latter (the outer) returns by means of the bronchial veins. This, in brief, is the result of the author's investigations. They are confirmatory of those of Adriani. The *mode* in which the bronchial and pulmonary vessels communicate is stated differently by different authors. Some suppose that the blood of the bronchial arteries is poured directly into the pulmonary *artery*, with the venous blood of which it admixes, and like which, traversing the respiratory plexus, becomes arterialised before it reaches the left auricle. On this supposition the blood entering the left auricle would be purely and exclusively arterial. By other anatomists — of these Rossignöl is the most prominent * — it is contended that the bronchia

* Physiol. Anat. by Todd and Bowman, p. 393. vol. ii.

† In an excellent paper recently read before the Royal Society (June 9th, 1853), Dr. Heale states this fact still more strongly. He denies that the vascular plexus, distributed over the walls of the bronchial tubes, is derived at all from this system of vessels, but from the pulmonary *rete*. I have repeatedly remarked, that the *bronchial* plexus cannot be injected from *the aorta*. I ascribed the circumstance always to some imperfection in the attempt. It will be seen in the text further on, however, that my injections prove the presence of a *bronchial* plexus on the *exterior* of the bronchial tubes, though not on the *interior*.

* "Dans les injections faites par les artères bronchiques, le liquide revenait en abondance par les veines pulmonaires, en bien moindre quantité par les veines bronchiques, et on n'en retrouvait aucune trace dans les rameaux de l'artère pulmonaire."

blood is poured into the pulmonary system at the *left* side of the respiratory *rete*. The current, therefore, entering the left auricle is not *pure* arterial blood: it is alloyed by the venous rivulet received from the bronchial system,— a reptilian characteristic traceable in human organisation.

By a third class of observers it is said, that the *capillaries* of the pulmonary and those of the bronchial system of vessels intimately inosculate. The precise solution of this question is difficult, in consequence of the readiness with which an injection thrown into one vessel will pass into another by *extravasation*. Other anatomists suppose that the three above-described modes of communication actually exist. It is certain that these two systems *do* communicate, and that only *a part* of the blood of the bronchial arteries returns by the bronchial veins. More recently, a new aspect has been given to this controversy by the statements of Dr. Heale, to the effect that the bronchial and the pulmonary systems of vessels do *not in any manner or degree* communicate. He maintains, on the evidence afforded by his injections, that the vascular web of the air-cells *extends*, and is prolonged over the internal surfaces of the bronchial tubes. Dr. Heale assigns to this *extension* of the *rete mirabile* the power of prolonging the aëration of the blood. This is impossible. The bronchial tubes, the minutest, are internally lined by a dense ciliated epithelium. Such epithelium does *not* exist on the true *capillary* parts of the lungs of any vertebrated animal. Where there is *ciliated* epithelium, a universal principle of structure requires in the *higher vertebrated* animals that the function of breathing should be suppressed. This principle, however, does not obtain in respiratory organs of the invertebrata, and in the bronchial organs of lower vertebrata.

Respiratory Organs of Birds.

The lungs of birds are two in number, symmetrically developed, flattened, and irregularly triangular in figure. They are fixed, by means of areolar tissue, to the ribs and vertebral column, from the inequalities of which they receive deep impressions. They extend from the second dorsal vertebra as far as the kidneys, and laterally to the junction of the vertebral with the sternal ribs. In their fixed position under the back and near the centre of gravity, they contrast strikingly with the lungs of mammals, which float loosely in the thoracic chamber. In colour they are blood-red, and in general texture they are more fragile than the lungs of mammals. They are not divided by deep fissures into lobes, like the mammalian lung; lobuli, however, exist, although more lengthened in form than those of the mammal lung. In the former, as in the latter, a

Fig. 225.

A. *Lobule of the lung of a Bird represented in ideal longitudinal section.* (*Original.*)

a, a, a, primary bronchi maintaining a uniformity of diameter and terminating cœcally; *b, b, b,* secondary bronchi, maintaining also a regularity of diameter and opening into a dense cubic labyrinth of blood-vessels *c, c.*

B. *A small piece of the ultimate portion of the lung, representing the arrangement of the ultimate respiratory capillaries.*

lobule is a smaller lung. All its parts are complete. The lobuli are embraced and isolated by membranes of areolar elastic tissue. A pleural investment embraces their sternal aspects, and an aponeurosis, proceeding from the diaphragmatic muscles below, blends its fibres with those of this covering. The trachea, after a course in the neck varying with the length of this part, at its entrance into the lungs, divides into two primary bronchi, one for each lung. At the place of this bifurcation there exists, in most birds, a complex mechanism of bones and cartilages, moved by appropriate muscles, and constituting the true organ of voice. This part is known as the inferior larynx.* The trachea is composed of rings of cartilage which are *not* deficient at the posterior third of the circle, as in quadrupeds. The successive rings are linked together into a cylindrical form by means of a highly extensile and elastic membrane. The whole cylinder is embraced in a second concentric cylinder of muscular fibre which belongs to the voluntary or striped variety. In this particular it differs from the trachea of mammals. In the latter, only the deficient portion of the rings is composed of

" Par les artères pulmonaires, l'injection revenait en entier par les veines correspondantes et *jamais* par les artères bronchiques."

" Enfin, l'injection poussée par les veines pulmonaires remplissait tous les autres vaisseaux sanguins du poumon, c'est-à-dire, l'artère pulmonaire, les artères et les veines bronchiques."—Rossignol, Op. cit. p. 64.

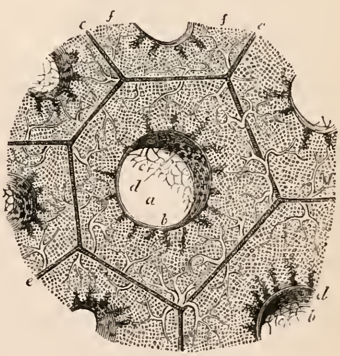
* See arts. LARYNX, VOICE, and art. AVES.

muscular fibre, and that too of the involuntary or unstriped kind. This muscular layer in birds extends from the superior larynx to the commencement of the bronchi : these latter are, however, unsupplied by muscular fibres. They are exclusively membranous.* The bronchi in the case of birds, on entering the substance of the lungs, divide and subdivide without decreasing in diameter (*a*, *a*, *a*, *fig.* 225.) Patches of cartilage appear in the parietes only of the largest order of these tubes. They are distinguishable into two principal classes: those, first, which course superficially along the inferior or sternal surface, and which terminate by wide openings in the thoracic and abdominal air-receptacles. This class of tubes is perforated by the inter-cellular passages only on one side, the other being strengthened by cartilaginous semi-rings. The deep bronchi, resembling cylindrical tubes, traverse the lungs in many directions, and freely communicate with each other, not, however, to form a network, for they run in nearly parallel directions. These tubes are always patulous on dissection, and seem incapable of contraction and dilatation. They are lined internally by a well-marked ciliated epithelium. The submucous tissue in the true bronchi is strong and dense, composed chiefly of elastic fibres, *none* of a muscular character. It constitutes a distinct fibrous layer, like that which lines the trachea of quadrupeds. Those bronchi which do not end in open orifices on the surface of the lung terminate cœcally. These cœcal extremities are perfectly defined by a prominent lining of fibrous and mucous membrane. It was first proved by Mr. Rainey that in the lungs of birds the mucous membrane does not extend inwards in the direction of the interior of the lungs beyond the limits of the bronchi. By the words *mucous membrane* Mr. Rainey desires to indicate that flocculent covering which is so well seen in his *injected* preparations. By this observer it is maintained that all parts of the lungs of birds *beyond* the extremes of the bronchi are literally devoid of all epithelial covering whatever, the extreme capillary vessels being included in nothing but their own proper tunics. It has been already shown that Mr. Rainey has mistaken the cessation of the *ciliated* epithelium at the ends of the bronchi for the termination of all the other elements of this covering. The *apparently* naked vessels of the air-cells are *really* invested by a hyaline epithelium, coinciding with that which, in the instance of reptiles, will afterwards be described. The abrupt termination of the bronchial tubes marks the abrupt commencement of the intercellular passages. These passages contrast remarkably in structure with the bronchi. The membranous walls of these parts are reduced to the utmost state of thinness; those of the former are furnished with cylindrical epithelium and a dense fibrous coat. But, what is extraordinary, the dense mass of vessels which bound these passages are *not* joined together into a continuous partition. Each vessel is separate from and unconnected with those adjacent. "A wall" thus constructed is at every point *between* the vessels permeable to air. These "intercellular passages" (*b*, *b*, *b*, *fig.* 225.) arise, with singular uniformity, from the sides of the bronchi, at right angles to the axes of the latter. This is so constant as to become a characteristic point of structure in the bird's lung.

* See art. AVES, by Prof. Owen.

The "spaces" between the vessels forming the walls of the intercellular passages lead to no definitely bounded *cells* or chambers. They lead only to the *interval* which divides the contiguous bronchi from each other (*c*, *c*). This *interval* is filled densely with the ultimate pulmonary vessels. (B, *fig.* 225.) It was first determined by Mr. Rainey that these vessels, in the bird's lung, are arranged in a peculiar manner. They do not form *plane* reticular definitively bounded air-chambers. Each ultimate capillary crosses an air-space of its own. It is thus *surrounded* by air. The ultimate vessels interlace and interloop in every direction, forming a *cubic* mass of capillaries *permeated everywhere by the air.* The apparently naked loops of the ultimate vessels may be seen projecting into the areas of the intercellular passages. Nothing can be conceived more mechanically perfect than this arrangement of the vessels for the exposure of the blood to the operation of the air. The latter is in immediate contact with each individual vessel (B, *fig.* 226.) It *surrounds* the blood-current borne

Fig. 226.



Slightly oblique section through a bronchial tube. (After Rainey.)

a, cavity of the tube; *b*, its lining membrane, containing blood-vessels with large areolæ; *c*, *c*, perforations in this membrane, where it ceases at the orifices of the lobular passages (*d*, *d*); *e*, *e*, spaces between contiguous lobules, containing the terminal pulmonary arteries and veins supplying the capillary plexus (*f*, *f*) to the meshes of which the air gains access by the lobular passages.

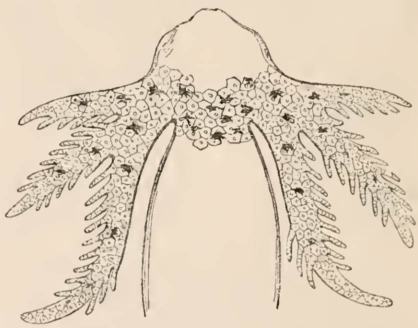
by the latter. Every part of the circumference of this current, less than $\frac{1}{9600}$ of an inch, is under the *direct* agency of the aerating *element*. In the bird's lung there exist, therefore, no *air-cells*.

It is argued by Mr. Rainey that the *ultimate vessels* in the bird's lung, as in the mammal's, are literally *naked;* that is, that they have no other covering whatever than their own proper coats, of which at irregular intervals the cell-nuclei may be distinguished. In other words, that the epithelium, so perceptible on the bronchi, is *not under any shape* continued beyond the termination of these tubes. To this view it has already been objected that it is at variance with all analogy; the branchial and pulmonary vessels of fishes and amphibia are provided, as will be subsequently shown, with pavement epithelium, the scales of which may be seen to be continuous with those of the ciliated division of the membrane; that a law of anatomical structure applying to the respiratory organs of the lower vertebrata must also govern that of the higher. It *is* impossible to demonstrate on the *injected vessels of the bird's lung* the presence of a separate investment of epithelium. The vessels *do* appear to be literally naked. But in the recent structure, in their sections through the bronchi and intercellular passages, it is perfectly easy to the practised eye to trace the epithelium of the bronchi over the larger vessels amid the intercellular passages just before the former break into the mass of the ultimate capillaries. The continuity of the *pavement* epithelium of the larger vessels with the *cylindrical* of the bronchi may be undoubtedly traced by the eye. Now, what is true of the larger vessels is very probably true also of the smaller. Although, therefore, it cannot be directly *proved* at present that in the bird's lung the ultimate capillaries, as in the branchiæ of fishes and the saccular lungs of amphibia, are invested by a separate epithelium, the conclusion first stated appears at present to be most reasonable and most in accordance with analogy. In these examinations it is important not to mistake the *outline* of the red corpuscles in the vessels for that of the epithelial scales on their parietes. According to the measurements of Mr. Rainey the *areolæ* between the capillary vessels, which in the bird's lung are the real air-spaces, — equivalent to air-cells, — are generally smaller in diameter than the capillaries themselves, and average in diameter about $\frac{1}{9600}$ of an inch. An epithelial cell taken from the lining membrane of the bronchi in a pigeon measures in length $\frac{1}{800}$, and in breadth $\frac{1}{3300}$. It is therefore certain that, as Mr. Rainey contends, epithelium of *such* magnitude *could* not, by physical possibility, line spaces the diameter of which did not exceed $\frac{1}{9600}$ of an inch. The error here committed consists in overlooking the difference between the dimensions of the *cylinder* epithelium which lines the bronchi, and those of the wondrously attenuated hyaline epithelium which belongs to the true respiratory, capillary, areas of the lungs of birds, reptiles, and mammalia. A similar distinction between the epithelium which lines the cæcal *extremities* of glandular ducts, and that covering the merely convective or excretory stages of the *same* ducts, obtains in nearly all the simple and compound glands of the animal body. How singular if a principle so wide-spread should be violated in the instance of the lungs!

Respiratory Organs of Reptiles.

Temporary branchiæ of Amphibia. — In the life of all batrachian reptiles, the period which immediately follows the emergence of the young from the ovum is remarkable for the existence of organs capacitating the animal to live in water. In different genera these organs vary in duration of existence. The larvæ of the frog retain the external branchiæ only for a few days, after which these organs become internal. Those of the toad remain in the egg state for a longer, and in that of the fish condition for a shorter, time than those of the frog. The tadpoles of the terrestrial salamanders of this country retain the external gills only for a brief interval, early assuming an exclusively atmospheric life. Those of the aquatic species, exemplified in the familiar tritons of our pools, carry the external branchiæ for a much longer period, affording thus, an opportunity for the study of the structure

Fig. 227.



Head and branchial appendages of the larva of the Water-newt (Triton aquaticus vulgaris). (Orig.)

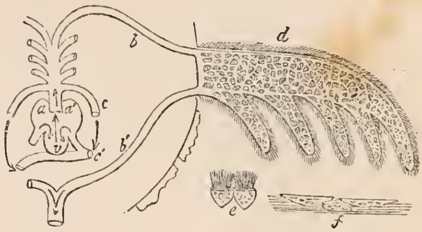
The branchiæ are enveloped in a prolongation of the general cuticle of the body. The cells of the epithelium covering the gills are, however, reduced to a state of great attenuation, compressed into scales, and polygonal in outline. The nearer the period of transition from the larva to the perfect reptilian type, the more intimate the resemblance between the epithelium of the branchiæ and that of the general body. For some time before their obliteration, the branchiæ cease to be distinguished by ciliary vibration. This results from the change which gradually occurs in the anatomical characters of the component cells. The branchiæ in the larva of the newt consist of a trilobed extension of the cuticle at either side of the head, the two posterior lobes, which, in figure, resemble compressed finger-like processes, presenting on either side secondary projections, by which the respiratory area is multiplied. In relation to the size of the body, they are larger than those of the larva of the frog.

and function of these appendages. The genera *syren*, *proteus*, and *menobranchus* are those only in which the external gills are persistent throughout the whole term of adult life. Whether temporary, as in the caducibranchiate, or persistent, as in the perennibranchiate genera, the branchial organs of amphibia are supported by no skeletal framework analogous to that which sustains the soft parts of the breathing apparatus of fishes. They are, essentially, only "productions," under a modified form, of cutaneous structures. Contemplated only as a mechanical contrivance, whether provisional or permanent, upon which devolves the most important function in the animal economy, it demands a more minute investigation than it has hitherto received at the hands of anatomists.

The cartilaginous arches erected on the hyoid bone do not entirely disappear until the *internal* gills have ceased to be distinguishable. The circulating system of the decidual branchiæ consists, in its earliest stage, of a simple artery and vein; that is, a loop of one vessel. As the larva grows these two vessels become separated by an intermediate system of capillaries. In the latter phase they offer no remote analogy to the vascular apparatus of the branchiæ of fishes. The cardiac centres are composed only of a right auricle and one undivided ventricle; the left or pulmonary auricle remains unevolved until the organic necessities attendant on growth create a necessity in the system for the exercise of the pulmonary functions. The left auricle is then superadded, and the chamber of the ventricle is partially divided by a median partition, and the embryonic organism reaches the maximum limit of development. The pulseless ventral artery, the resultant of the united afferent vessels of the branchiæ, undergoes obliteration through disuse. These general observations form no irrelevant introduction to a more special examination of the branchial organs.

Temporary external Gills. — The larval branchiæ of the frog and toad are less enduring and less complex than those of the salamandridæ. From the earliest almost to the latest moment of their existence they are furnished with a ciliated epidermis. The gills are not specially ciliated. The whole cutaneous surface in the larva of the frog and toad is similarly endowed. The cilia are in active play for some time *before* the larva emerges out of the egg: an admirable instance of foresight in the provisions of nature. The covering of the external gills of the ranidæ is strictly cutaneous. In this situation, as everywhere else, the epidermis betrays its real nature by the presence of pigmental cells. It is little less dense than the ordinary covering of the body. Nor does the vascularity of these temporary branchiæ much exceed that of the rest of the cutaneous surface. These facts proclaim their provisional character. At first they consist of a single minute lobe. This increases into two and then into several. They are cylindrical, not flattened, processes. They bear a *single* vessel returning upon itself. In this particular of ultimate structure they differ from the branchiæ of the salamandridæ. In these a *capillary* net-work is constructed between the artery and vein. This greater

Fig. 228.



One of the gills of the Newt viewed transparently. (*Original.*)

a indicates the right auricle, which with *v*, the ventricle, constitutes the heart of the true fish; *a′* shows the left or pulmonary auricle, which, being superadded to the two former parts, raises the cardiac organ to the reptilian standard, marked by the presence of two auricles and one incompletely partitioned ventricle; *b*, *b′*, denote the circuit of the branchial system in conformity with the pisciform type. This system of vessels being obliterated during the metamorphosis of the larva, the pulmonary vessels (*c c′*) enlarge, the rudimentary lungs at the same time expand, the associated auricle grows in muscularity and dimensions, and the fish rises to the grade of an air-breathing reptile. *d*, is an enlarged view of the gill of the larva of the newt soon after its escape from the ovum. Secondary processes (*d*, *d*, *d*, *d*) are extended backwards, which materially multiply the surface. The whole gill is clothed with ciliated epithelium, the cells of which lose their cilia, and become *non-vibratile* for some time before the cessation of the branchial breathing, and the oblong-cilia-bearing cells (*e*) are transmuted into epidermal scales (*f*) entirely destitute of cilia.

elaboration coincides with their longer duration. What is ephemeral in purpose is temporarily formed. This is nature's workmanship. They consist literally of small prolongations of the skin, which is everywhere, as here, ciliated. At the moment of their fullest development, the larval branchiæ of the frog consist of four filamentary lobes. These are sessile upon the body or stem of the branchiæ; they are somewhat granular on the surface, and slightly irregular in form. There is also frequently a short additional branch at the base of the posterior one. In these interesting organs the movement of the blood is readily demonstrated. It is a beautiful spectacle. It advances in a single current along one side and returns along the other. No sooner have these exquisite organs attained their greatest development than they begin to diminish in size. They become obtuse, and are gradually so reduced as to be withdrawn within the branchial cavity, and concealed by a little operculum of the integument. The *nature* of this change of structure, which attends the transition of the branchiæ from the external to the internal condition, has never yet been defined by anatomists. It will be immediately described.

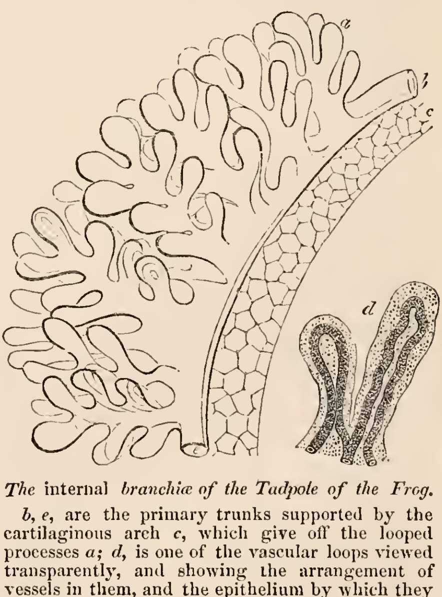
The *external Gills of the Salamandridæ* exceed the former in size, in the number of the appended lobules and in the complexity of their vascular system (*figs.* 227, 228.) Like those of the ranidæ they are clothed in a vibratile epidermis, numerously starred by pigmental cells, in common with the rest of the body. For some time before the decadence of these organs in the larvæ of the triton they cease to exhibit the phenomenon of ciliary vibration. The vibratile epidermis undergoes a change by which the ciliated cell becomes succeeded by the simple. This event foretells the approaching extinction of the parts. In their earliest condition the branchiæ of the newt discover only four minute simple cylindrical filaments. Each grows in length and thickness, and throws out from the inferior surface a *double* row of pectinated processes. These are more complexly constructed than the primitive filaments. They carry not only an afferent and efferent trunk, but an elaborate plexus of capillary vessels. The pigment cells are limited in their distribution to the larger lobes, and to the line of the larger vessels. The epidermis of the secondary processes of the branchiæ is reduced to extreme tenuity. Through it the eye readily tracks the movements of the individual blood corpuscles on the branchial capillaries. These elliptical bodies move like a boat, their long axes coinciding with that of the channel in which they are travelling. Sometimes several proceed abreast. The diameter of the vessels of the temporary branchiæ is greater than those of the lungs. In general terms it can be confidently stated that the quantity of blood circulating in the temporary branchiæ of the amphibia, at the period of their maximum development, is far less in relation to the amount contained in the whole body than that which the lungs, when fully formed, are capable of carrying. This inferior amount of blood is physiologically expressive of an inferior functional power in the case of the temporary organs. Their respiratory function is really only supplemental to that of the whole body. The whole cutaneous surface, as in the Næmatoid annelids, is richly ciliated. It is organised like the branchiæ. On these parts, however, the epidermal layer is not so attenuated as that with which the branchiæ are invested. On these latter there *is*, however, a very perceptible epidermal covering. Its scales exhibit the ordinary hexagonal figure.

This demonstration, which dispels all doubt, establishes the physiological principle, that the *presence* of epithelium is compatible with the *respiratory* office of the part which it clothes. This *law* prevails throughout the class of fishes; it has also been reduced to actual fact by the author throughout the whole sub-kingdom of the invertebrata. But it must not be forgotten that its office on the breathing organs is almost exclusively mechanical. In no known example among vertebrated animals does the epithelial investment of a respiratory surface develop itself into *any* of the forms of a secreting organ. No "follicles" are, at any time or under any circumstances, discovered on these localities, in this class of animals, but in the invertebrata follicular glandules are constant on the surfaces of the respiratory organs. The constituent scales are therefore functionally *passive*. Nuclei and a granular protoplasm would find no purpose to subserve if they were present in a highly developed form. Thus is exemplified the law of "demand" and "supply:" disuse entails attenuation on all living structures. Either the gases by which the epidermis of respiratory localities is traversed *suppress* the glandular office of the scales, or these latter, from the first, receive a special organisation. The scales of the branchial epithelium contain nothing but a pellucid fluid. This fluid *condenses*, fluidifies, the respiratory gases *in transitu*. *This* is the office of the refined covering under study. The "principle" that the epithelium of the breathing organs is required by the physical conditions of its office to be reduced to the state of the utmost thinness receives new proofs from the study of the internal branchiæ.

From all that is known it is probable that in minute structure the branchiæ of the perenni-branchiates conform to the plan of the temporary organs just described. The general arrangement of the primary branchial vessels and the structure of the heart are identical.

The internal temporary Branchiæ of the Amphibia. — The process by which these organs are withdrawn into the interior of the branchial chamber is not simply that of shortening. It is the labour of a *new* organisation. The internal gills of the tadpole differ in type

Fig. 229.



The internal *branchiæ of the Tadpole of the Frog.*

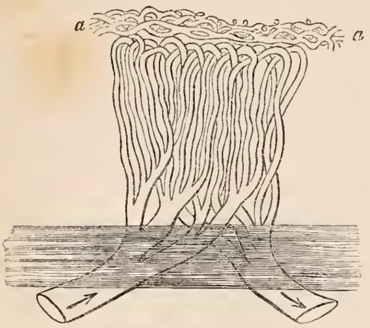
b, e, are the primary trunks supported by the cartilaginous arch *c*, which give off the looped processes *a*; *d*, is one of the vascular loops viewed transparently, and showing the arrangement of vessels in them, and the epithelium by which they are covered.

of structure from the external. The ultimate vessels of the latter are differently looped.

In both they are simple loops, but a distinction is obvious; so evident as to render it impossible that the transition from the exposed to the concealed state of the branchiæ can consist in a bodily retractation. On the *external* organs, preparatorily to their disappearance, the vibratile cilia first cease, the epidermis then increases in density, the meshes between the blood-capillaries enlarge, and the vessels become obliterated. These declining changes are not limited to the extreme distal ends of the branchial lobules. They occur simultaneously on every part of the surface. Temporary arches (*c*) of delicate cartilage now arise within the branchial chamber. It is from the convexities of these arches after the manner of the pisciform type that the *new* vessels (*a*) of the internal temporary gills proceed. They are appended under the character of delicate flocculi. Enlarged, they appear as minute digitations. Each carries a looped vessel, and is *loosely* invested with a delicate membrane (*d*). This membrane belongs to the mucous, not to the epidermal, class; and yet it differs in a striking manner from that which lines the rest of the branchial chamber. *Nowhere is it ciliated.* That covering the branchial vessels is remarkably thinner than the parietal portion. The former, however, *is true epithelium.* Its constituent scales are distinctly traceable by their outlines, though they are as structureless as a basement membrane. It is not often that it happens that the epithelium of a breathing organ overlies, as in this instance, perfectly homogeneous parts. Nothing but the proper coats of the vessel lie underneath. They are literally structureless and hyaline. The cells of the superficial epithelium, therefore, admit of indisputable definition. It is not "basement membrane," but epithelium, though attenuated, that here invests the respiratory vessels. By this demonstration a *principle* is established. Epithelium is *not* supplanted by any other structure on the organs dedicated to respiration. No other instance, however, is known within the limits of the vertebrate kingdom in which this epithelium is ciliated, than that afforded in the case of the temporary external gills of the Amphibia. On those of fishes these motar organisms do not exist. Wherefore this distinction? Why should they exist on the external and not on the internal gills? It is not a *law* of the mucous membrane that they should *not* exist, for they occur in other tracts of this same structure. These are questions of ultimate design which it is not given to science to answer.

Air-bladder of fishes. — This organ represents the prototypal form of "the lung" in the animal kingdom. It is present in nearly all osseous fishes. It is always tensely filled with gas. In that of marine fishes, oxygen predominates; in that of fresh water, nitrogen. Humboldt found the gas in the air-bladder of the electric gymnotus to consist of 96 parts of nitrogen, and 4 of oxygen. Biot found 87 parts of oxygen, nitrogen, and carbonic acid in the deep Mediterranean fishes. No hydrogen has ever been detected in this organ. It occupies the roof of the abdomen, between the kidneys and chylopoætic viscera, and sometimes (*gymnotus ophiocephalus, coius*), beneath the caudal vertebræ to nearly the end of the tail. In some species of *diodon, tetradon, dactylopterus, pemelodus,* and *poianotus*, it is bifurcated. In *arius gagora, polypterus and lepidosiren,* it is divided lengthwise into two bladders. In the *cyprinidæ* and *characinidæ* it is divided transversly into two communicating compartments. Many other varieties of form occur. (*Vide* art. PISCES.) The proper walls of the air-bladder consist of a shining silvery fibrous tunic, the fibres being arranged for the most part transversely and circularly, and in two layers. They are contractile and elastic. This coat yields the finest gelatine. Its fibres belong to the white variety: they "swell" under the action of acetic acid. A stratum of vessels is interposed between the mucous membrane and the fibrous layer. The meshes formed by these vessels are considerably larger and more oblong than those of the pulmonary capillaries. In the latter instance the meshes *exceed* the vessels in diameter. The arteries of this organ are derived sometimes from the abdominal aorta, sometimes from the cæliac artery, sometimes from the last branchial vein; and in the lepidosiren they are continued from the aortic termination of the two non-ramified branchial arteries, and therefore convey *venous* blood to the cellular, lung-like, double air-bladder (Owen). The veins of the air-bladder return, in some fishes, to the portal vein; in some to the hepatic vein; in some to the great cardinal vein; and in the lepidosiren, they penetrate by a common trunk the great portal vein formed by the confluence of the visceral and vertebral veins of the trunk. In the *protopherus* and ganoid fishes the vessels of this organ form no *retia mirabilia* and vaso-ganglions, but rather a diffused capillary network, more close and rich in the anterior than the posterior part. In the osseous fishes, several varieties of the vascular system of this organ occur. That of the carp forms tufts of capillaries throughout the whole interior of the organ, a variety of which tufts occurs in the pike. The perch and cod exhibit a vaso-ganglion, a body peculiar to the air-bladder of fishes. In the cod-fish, a large artery, a branch of the cœliac, and a still larger vein, which empties itself into the mesenteric, perforate together the fibrous tunic of the bladder. Before they reach the inner surface, they divide into some branches which then radiate and subdivide upon the mucous membrane. The arterioles frequently anastomose with each other. Both are inextricably interwoven, and form the basis of the so-called "air-gland," which is essentially a larger "bipolar rete mirabile" (Müller), or vaso-ganglion. In the cod the ultimate vessels of this gland have a loop-like arrangement, their free surface (*a a*), being covered over with another layer of vessels and epithelium This organ, however, is further composed of a number of pecu-

Fig. 230.

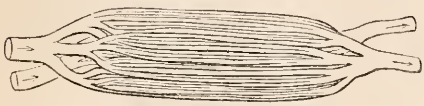


Plan of blood-vessels in the gland (aërogenic?) of the air-bladder of the Cod-fish, showing the simply looped character of the vessels. (Original.)

a, *a*, indicate a stratum of fibres, vessels, and epithelium lining the internal surface of the gland in common with the whole interior of the air-bladder.

liarly arranged, elongated corpuscles, which descend in two rows from each vascular branch, and are bound together by a loose cellular tissue: the corpuscles are beset with fine villiform processes. Thus it should be noticed that the *veins* as well as the arteries concur to form the vaso-ganglions. The vaso-ganglions of the eel and conger are placed at the sides of the opening of the air-duct, are "bipolar," and consist of arteries and veins; their efferent trunks do not ramify

Fig. 231.



Plan of the blood-vessels in the glands of the air-bladder of the Eel. They consist of straight parallel ultimate vessels of uniform diameters, of arteries, and veins, carrying streams of blood moving in opposite directions. (Original.)

in the immediate margin of the vaso-ganglion from which they issue, as in the vaso-ganglion of the cod, turbot, acerine, and perch, but run for some distance before they again ramify to form the common capillary system of the lining membrane of the air-bladder. In the parasitic and suctorial dermopteri and pleuronectidæ and ray-tribe the air-bladder does not exist.

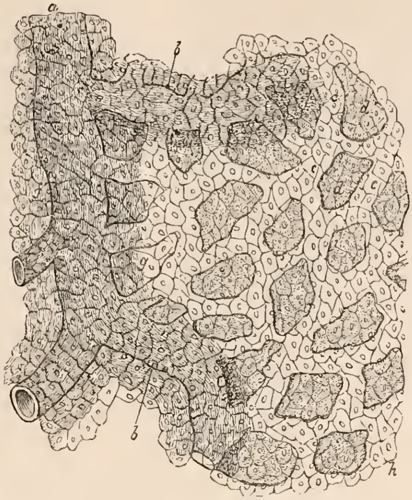
The *ductus pneumaticus* exists in the *eel*, *sturgeon*, *amia*, *erythrinus*, *lepidosteus*, *lepidosiren*, *polypterus*. It is remarkable that in these fishes the vaso-ganglion is not developed. "Under all diversities of structure and function the homology of the swim-bladder with the lungs is clearly traceable; and finally, in those orders of fishes which lead more directly to the reptilia — as, for example, the salamandroid *ganoidei* and *protopteri*—those further modifications are superinduced by which it becomes also analogous in function to the lungs of the air-breathing amphibia." *

The Lungs in the Batrachia.—In the ichthioid amphibia there exist two long membranous pulmonary sacs, extending, like the air-bladder of fishes, far backwards into the cavity of the abdomen, above the other viscera, but freely moveable in the cavity of the peritoneum, and invested with this serous membrane. They consist of smooth plane-walled sacs, and communicate with the pharynx by means of their membranous *ducti pneumatici* or tracheæ. This simple condition of the lungs occurs in a permanent form in the salamandridæ. Each sac is provided with a pulmonary artery, which runs in a straight course along the outer side of the organ. From this vessel, branches proceed with great regularity at right angles and at definite distances. From the midpoint of the space between the arterioles, a venule arises to run round the opposite semi-cylinder of the organ into the chief trunk of the pulmonary vein. In consequence of this regularity in the distribution of the arteries and veins, the true capillary interspaces present a regularity of area. It follows from this arrangement that each drop of blood, in its passage from the extreme artery to the extreme vein, undergoes in every part of the lung the same *quantum* of aeration. It is commonly supposed, by comparative anatomists, that the simple lungs of the *salamandridæ* present a perfectly smooth and uniformly plane surface internally, such that every spot participates with equal activity in the office of aerating the blood. This, however, is not the case. The *septa* which, in the case of the frogs and toads, divide the internal superficies into *cells*, exist in a rudimentary state, but *unquestionably* in the lung of the newt. *They are indicated by intersecting lines of vibratile cilia.* They coincide chiefly with the principal branches of blood-vessels. Bundles of elastic fibres also *run parallel* with the vascular trunks, which confer upon these delicate organs an uncommon amount of elasticity. To the next point in the minute structure of the lungs especial

* R. Owen, Cat. of Phys. Ser. of Coll. Sur. 4to, 1832-40; Müller, J., Vergleichende Anatomie der Myxinoiden: Abhand. Akad der Wissenschaften zu Berlin, 1834; Agassiz, Hist. des Poissons Fossiles, 1833-45; Cuvier et Valenciennes, Histoire Nat. des Poissons, 1845; De Blainville, Annales des Sciences Naturelles, 1837; Bojanus, Versuch einer Deutung der Knochen in Kopfe der Fische, in Oken's Isis, 1818; Yarrell on British Fishes, 8vo, 1836; Paley, Nat. Theol. 8vo, ed. 10. 1805; Brescher, Récherches sur l'Organe de l'Ouie des Poissons, 1838; Monro, The Structure and Physiology of Fishes explained and compared with those of Man and other Animals, fol. 1785; Scarpa, De Auditu et Olfactu, 1789; Hunter, Obs. on the Animal Economy, Palmer's ed., 1837; Ratke, in Die Physiologie von Burdach, 8vo, i. 1826; Allen Thompson, Jameson's Journal, 1830-31; Duvernoy, Sur le Mécanisme de la Respiration dans les Poissons, in Ann. des Sc. Nat. 1839; De la Roche, Obs. sur la Vessie Aërienne des Poissons, Ann. du Muséum, t. xiv. 1809.

attention is invited. The conclusions hereafter to be drawn will be found opposed to

Fig. 232.



A small portion of the lung of the Newt laid open and examined by transmitted light, under a high power, such that only the surface (internal or mucous) is in focus. (Original.)

a, a leading branch of the pulmonary artery, giving off at very regular intervals which break at once into the true capillaries *c, c, c.*; *d, d, d,* denote the parenchymous islets which fill up the meshes of the capillary plexuses. (They are the true *pulmonary parenchyma.*) *g*, marks the abrupt line which abruptly limits the distribution of the *ciliated* epithelium, which follows the larger vessels in tracts; *d, c, c, c,* coinciding with the true respiratory or capillary areas of the lung, are seen to be destitute of *ciliated* epithelium.

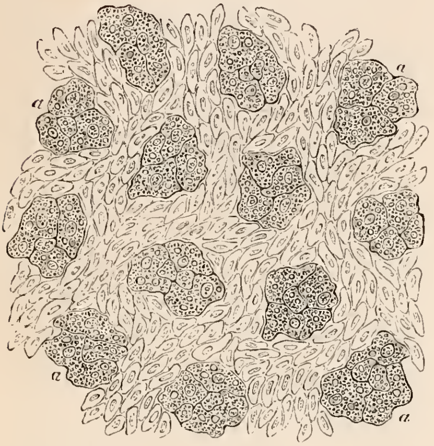
the views of Mr. Rainey. This excellent observer* has affirmed the principle that, on the true breathing portions, or capillary segments of the lungs, there literally exists no epithelial lining of any description whatever, the vessels being as literally naked. To this "principle," deliberately enunciated and supported by elaborate "proof" by an acute and truthful observer, many anatomists have yielded implicit assent. First, it is here objected that such a "principle" violates directly all the lessons of analogy. Analogy! Is not demonstration better than analogy? In the science of organised beings, the connected reasoning founded on analogy cannot be despised. The closest scrutiny in individual instances may miss the truth. The manifold illusions of the microscope may readily mislead. Analogy supposes a mass of *cumulative* evidence. The general law neutralises particular errors. In no instance whatever, either in the vertebrate or invertebrate kingdom, has it been proved, in the course of the present extended inquiry, that the vessels of a real breathing organ can exist under a perfectly "naked form." What is true of invertebrate animals as an organic law cannot be untrue of the vertebrate. The gills of fishes are furnished with a very marked epithelial covering. The temporary branchiæ of the amphibia are clothed with epidermis. The air-bladder is provided with an epithelial lining, the cells of which admit of ready and conclusive demonstration. Why should it not exist in the case of the true pulmonary structures? No *reason* can be imagined; but the *fact* that it does *not* has been affirmed by Mr. Rainey. Mr. Rainey's observations were instituted upon *injected* preparations. This is the source of the error into which he has fallen. If the lung of the newt be carefully, but quickly, laid open, covered, but *not pressed*, with a thin slip of glass, and examined under the microscope, it will be found that the vibratile cilia have a *limited* distribution. Under the favourable opportunities afforded by such a preparation it is perfectly easy to follow with the eye *the continuation of the epithelial cells* (*c, c, fig.* 232.) *beyond the limits of the ciliary areas* into the *true capillary or active breathing segments.* The ciliated portions of the epithelium (over the vessels *b, b*) exhibit a *flocculent* character, precisely as shown in the *preparations* of Mr. Rainey; while the areas immediately adjacent appear *smooth* or *naked.* But under the use of a higher power and a steady gaze the polygonal *outlines* of the epithelial scales can be *distinctly* discerned most readily between the islets of parenchyma (*d, d*). If this covering consist of "basement membrane," then basement membrane is composed of scaliform parts; but it is not. It is a true and real and unbroken continuation of the tracheal and bronchial mucous membrane. It is only the ciliary appendages to the cells that cease at a certain limit; the cells themselves continue to invest the *whole* superficies of the lungs. It is full of interest also to note that the epithelial scales which cover the *capillary areas* of the lung of the newt (parts which coincide with *air-cells* of the mammalian lung) lose not only the *external* appendages (cilia), but also their *internal* parts (nucleus and granules). This successive reduction leaves nothing but a *hyaline involucrum* enclosing a pellucid fluid. *This* is the *real* structure, supported indeed by a hypothetical basement membrane, by which the capillary areas of the pulmonary organs are invested. It finds a parallel in the transparent scales which cover the cornea.

In these ribless amphibia the operation of breathing resolves itself into an act of "swallowing" air. The glottidean chink is embraced by two minute semilunar pieces of cartilages and furnished with muscles for opening and closing the orifice. In the parietes of the lungs no trace of muscular fibres can be discovered; but elastic fibres are present everywhere among the vessels. It is by the agency of this elastic tissue, aided by the abdominal parietes, that the act of expiration is performed. The exterior of the lung is lined by peritoneum, the scales of which are much attenuated compared with those of other parts of the same membrane, as those

* Med. Chir. Trans. 1848.

of the internal lining. It is a curious fact that the *exterior* of the lung should be destitute of cilia, while they should be present on that of the liver in the newt. They are, however, on this last organ, limited to the margin. Nothing is more easy than to exhibit the living circulation in the lung of the newt. The

Fig. 233.



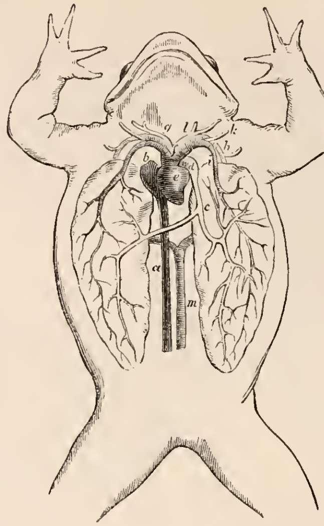
A small piece coinciding with the true capillary or respiratory area from the lung of the Newt, viewed by transmitted light under a high power. The blood-corpuscles in streams are seen in the spaces between the islets a, a, a. *Only these parts are in focus. The hyaline epithelium covering the near face of the picture is out of sight. The eye looks beyond it. In this fresh uninjected state the blood-channels do not appear to be bounded by separate and independent parietes.* (*Original.*)

a, a, a, are parenchymatous islets occupying the meshes of the capillary rete. They are composed of cells carrying nuclei and granules.

internal bore of the vessel viewed by transmitted light is much greater than the long diameter of the red corpuscles. The meshes (*a*, *a*) are mere points. The scene is one thick, rich, surpassingly beautiful network of moving blood.

In the *frogs* and *toads* the lungs consist of two large, short, and broad, slightly cancellated shining bags. They are situated on either side of the spine, at the roof of the abdominal cavity. They are remarkably elastic, like those of the newt. They are capable of slowly expelling their contents even after the removal of the abdominal walls, and of drawing themselves up into little hard balls on either side of the pharynx. They exhibit well the living circulation. The glottidean aperture communicates directly with the interior of the organ. There is, therefore, no trachea. The orifice of the glottis is surrounded by rudimentary cartilages somewhat further developed. The mechanism of breathing is the same in the frog and toad, in which, like the newt, the thoracic ribs are wanting, as in the salamanders. The steps of the process are, however, better studied in the frog. The outer surface of the lung in the frog is closely invested with peritoneum, the epithelium of which forms a thin pavement coating. This surface is destitute of cilia. In the frog, as in

Fig. 234.



Heart, vessels, and lungs of the Frog.

the newt, the edges of the liver are fringed with motile cilia. The pulmonary artery (see art. CIRCULATION), derived from the aorta, proceeds along the outer side of the lung. It lies immediately underneath the peritoneal epithelium. The very reverse course is taken by the large venous trunk on the opposite side. *This* lies in immediate contact with the internal or mucous surface. By this arrangement the contact of the blood with the air is prolonged. The contributory branches of the vein course along the *free* internal edges of the septa bounding the cells. The branches of the artery occupy the opposed *fixed* borders of the same septa. The flat surfaces, or sides of the cells, being the areas dividing the arteries and veins, are the scenes of the capillary segments. To this rule, of course, the eye, by close scrutiny, may detect many exceptions. By this distribution of parts, every spot of the internal superficies is functionally utilised. The *ciliary* epithelium is limited, in its distribution, to the margins of the cells and the lines of the larger vessels. The true capillary areas whereon alone respiration actively proceeds are covered only by a *hyaline* epithelium, the cells of which can only be distinguished by their outlines (*fig.* 232. *c*, *c*). The ciliated tracts, according to the manner already described in the lung of the newt, terminate by abrupt borders. The epithelial cell only is continued over the capillary areas. There prevails an *average* uniformity in the dimensions of these areas. Each particle of blood, therefore, in its transit from the artery to the vein across this area, is exposed, for the same period of time, to the influence of the air. In the lung of the frog and toad the *septa* support *two* layers of reticulate vessels, one on either side of a fibrous partition. A plane of vessels disposed in such a manner can only receive the influence of the aërating element on *one* side. This fact constitutes a real anatomical distinction between the lung of a reptile and that of a mammal. In this latter case the partitions of the cells are composed only of a *single* stratum, *both* sides of which are exposed to the air. By this simple mechanical provision the amount of the respiratory agency is everywhere doubled. In the structure of the reptilian lung the elastic fibre forms a predominant element. It is a substitute for ribs and other accessory apparatus of breathing. The lungs of the frog, relatively to the cubic capacity of their interior, present a much more extensive active surface than those of the Salamandridæ. Thus the purpose of "the cells" is fulfilled, of multiplying the operative surface. The "septa" project from the sides into the interior of the organ. In this respect they may be likened to the gills of fishes; for, like the latter, "they penetrate the surrounding medium." The lungs of ophidian reptiles are generally composed of true unsymmetrical, long cylindrical or fusiform sacs, extending from the pharynx far into the cavity of the abdomen, above the other viscera, and surrounded with the serous lining of that cavity. They are capable of containing a considerable quantity of air, which, when driven out with force, produces the "hiss" peculiar to the serpent. In some genera, as the coluber, typhlops and vipera, the lung of one side only is developed; in others, as the boa and python, the two lungs are symmetrically or equally developed. The lungs, in these families, communicate, by means of a long and narrow trachea, surrounded by incomplete cartilaginous "rings," with the back part of the tongue. In all ophidia, the lungs display internally, but *only* on the anterior and upper parts, an elaborate system of alveoli or cells, more like secondary lungs than air-cells. The posterior two thirds of the internal superficies are almost plane, or devoid of "cells," like the lung of the newt. The alveoli, traced from before backwards, become shallower and shallower, until at length they disappear. It thus appears that the serpent may store up in its lung a considerable volume of air which, slowly passing out over the vascular air-cells, prevents the carbonic acid, the effete product of the process, from contaminating the whole contents of the organ. Each "alveolus," separately examined by vertical section, is found to communicate by a single opening with the general chamber of the lung. Traced inwards, it divides and subdivides into secondary and tertiary tiers of "alveoli," each cell being *isolated* by dissepiments of which the structure is identical with those of the frog's lung already described. Each cell is a separate cavity. It does not communicate with those adjacent by openings in the septa. These septa are utilised in the outspreading of the vascular *rete*. Each septum, as in the frog, carries two layers of capillary blood-vessels, separated from each other and supported by an intermediate stratum of elastic tissue. In the mechanism of breathing, this tissue enacts an important office. Over the interior of the ophidian lung, like the batrachian, the *ciliated* epithelium is limitedly distributed. The true capillary areas which chiefly coincide with the flat sides and bottoms of the cells are clothed only with 'hyaline epithelium.' Everywhere throughout the interior of the lung, along the courses of the larger vessels, the borders of cells, or along lines of thickened tissue, the phenomenon of ciliary vibration may be readily detected. It is thus evident that the office of cilia is mechanical, if not to cause determinate currents in the *air*, at least in the *halitus* and fluid which, by accumulating, may obstruct the respiratory function of the capillary areas.

In the *boa* and *python* the length of the left lung is generally less by a third or half than that of the opposite side; but in *coluber*, *crotalus* and others, it is much smaller and quite rudimentary, appearing as little more than an obliterated appendage. The genera *Cæcilia* and *Amphisbœna* have the left pulmonary organ developed, and the right shortened: this arrangement probably varies according to the species. Vipers and other serpents possess only a single lung, which on that account is very long. The lungs of the *saurian reptiles* conform in character to those of the *ranidæ* and *salamandridæ*. They are elongated sacs, cellulated internally. They extend far back along the roof of the abdominal cavity. Like those of the ophidians, they are divisible into a cellulated and smooth or non-cellulated portion. The former is limited to the *upper* and anterior half of the organ; the latter to the inferior wall and posterior half. There may be a mechanical reason in this peculiar distribution of parts. The cells in the lungs of the saurians exhibit none of the regularity so characteristic of those of the ophidians. They are larger and more irregular. The partitions of the cells are more slender and more delicately-membranous.

The whole interior of the lungs in the higher saurians is multiplied into cells. An axis without definite walls, like a trachea, runs from one end of the organ to the other, as is the case in the lung of the turtle. From either side of this axis, large orifices lead to the more subdivided portions, or secondary and tertiary air-chambers. On the contrary, each lung in *Scincus officinalis* forms a single continuous cavity; but the *entire* surface of the parietes is cellulated by small projecting reticulate septa. The internal dorsal and anterior half of the lung of the chameleon is, as usual in the *sauria*, minutely cellulated. Further back the cells become larger, and the septa smaller, until at the posterior part the walls consist only of plane membrane both less vascular and less cancellated than the anterior. The cœcal extremity of the organ is drawn out into an appendage-like process, which reaches the farthest boundary along the roof of the abdominal cavity. These appendages may be aptly compared to the abdominal air-cells of birds which communicate with open extremities of the bronchial tubes. The "diaphragm" in the mammals precludes this interblending of the thoracic and abdominal organs, or the diffusion of air into any of the cavities of the body.

With reference to the *minute structure* of the lungs in the saurians, it coincides precisely with the account given of those of the *ranidæ*. Each *septum* consists of a central basis or framework of elastic fibrous tissue lined on either side by a reticulate layer of vessels. This plexus is again overspread by a "hyaline pavement epithelium." Rich *tracts* of ciliary epithelium may be discovered along the margins of cells, the course of vessels, and the lines of condensed structures. The double layer of vessels borne by each septum may be noted as a point of structure distinctive of the reptilian lung. The lungs of the *chelonian* reptiles are very voluminous. They extend over the whole dorsal part of the trunk as far as the pelvis. They are fixed by the pleura to the ribs, which also separate them from the cavity containing the digestive and generative organs. They are symmetrically developed on the two sides. Through the centre of each lung longitudinally an *un*walled axis extends from the anterior to the posterior extremities. This is the main road for the air-currents. From this axis, secondary passages, parietally cellulated, radiate towards every point of the circumferences of the organ. The ultimate cells are very capacious. They communicate little with each other. Each group has its common outlet, thus resembling a lobule. In the reptilian lung, however, there exist no lobules; an anatomical particular in which they are distinguished from that of all mammalia. It is a criterion of lower organisation. The vibratile cilia which line the nasal and buccal passages, the pharynx and œsophagus, the larynx and trachea of all reptiles are *most* remarkable for tenacity of life in the lungs of the chelonia. In the trachea of the turtle, along certain tracts of the lungs, the motion of cilia may be detected several months after death. The physiological value of the breathing process in any given animal corresponds, not with the volume of air inspired per any unit of time, but with the measure of the blood-surface exposed to its agency, the rate at which the blood-current moves, the numerical proportion of its red corpuscles,and the frequency of the respiratory movements. The small, but minutely, subdivided lung of the mammal presents a much more extensive surface for the outspreading of the *rete mirabile* than the very voluminous, but spacious-chambered lung, of the chelonian. The total volume of air inhaled by the mammal is less than that which the lung of the turtle is capable of containing; but in the former case it is more minutely distributed and divided; it is more effectually employed; the contact between it and the blood-web is far more extensive and intimate; while it acquires a higher temperature than in the latter. In these several particulars, cold differ from warm-blooded animals.

Respiratory Organs of Fishes.

The aquatic type, distinctive almost universally of the breathing organs of invertebrate animals, obtains also in the lowest order of the vertebrata. Fishes and the lower amphibia respire on the branchial plan. The difference between a gill and a lung rests more on apparent than real and ultimate grounds. In the last anatomical analysis this difference vanishes, and the eye is arrested only by the close structural affinities which reduce the two varieties to an essential unity of type. In *both*, the blood is exposed to the agency of the aerating element by means of reticulated vessels, furnished with distinct parietes, and presenting a diameter little in excess of that of the corpuscles of the blood; so that these latter must travel through the true respiratory capillary in a single series. This fact denotes the extreme measure to which the subdivision of the blood-stream is carried. It is a fundamental requirement of the breathing organ, that all structures interposed between the blood and the surrounding element should be reduced to the utmost degree of attenuation. Accordingly, it is found that the epithelium overlying the *rete mirabile* consists of a *single* layer of attenuated scales, perfectly destitute of those contained parts which give bulk and density. In no instance whatever within the limits of the vertebrata (excepting, as stated already, the branchiæ of the amphibia) are the true respiratory capillaries covered by a *ciliated* epithelium. This rule applies also to the branchiæ even of the higher invertebrata, such as the crustacea and cephalopoda. The gill of the fish differs from that of the crustacean in the extreme minuteness with which the blood current is subdivided, and in the existence of specially parieted vessels; conditions which denote an intensified measure in the function of breathing in the instance of the vertebrate animal. — In the blood of the vertebrata the floating cells are infinitely more numerous, relatively to the bulk of the fluid, than in that of the invertebrata; — a fact more expressive than the former of the greater activity of the respiratory process in the vertebrate than in the invertebrate animal.

It is an axiom in physics, that no gas is capable of passing through an organic septum without first assuming the fluid form. This axiom destroys the apparent difference between a gill and a lung. In contact with the gill the aerating medium is *already* fluid: in the case of the lung, it takes this condition only in *the act* of passing through the partition dividing the blood from the external medium. Between the gill of the fish and the true lung ofthe vertebrate animal there is discernible, however, this differential character, that in the former the epithelium clothing the active capillary segments forms a thicker layer (than in the latter. This is the only true and ultimate anatomical distinction between a gill and a lung.

The preceding general facts will form an appropriate introduction to the study of special details, on which it is proposed now to enter.

The Lancelet (Branchiostoma) occupies the first grade in the vertebrate series. It exhibits the branchial organs under the least complex terms. A capacious branchial sac, the dilated œsophagus, occupies the mid-portion of the body. It communicates with the exterior in front by means of a large œsophageal opening, and behind by a branchial outlet and a short intestinal canal. The parietes of the stomach display special provisions for breathing under the character of membranous duplications of the internal surface. These folds are invested with a vibratile epithelium. In this particular the branchiæ of this fish approach those of the lower molluscs, and depart from those of all other fishes. A convenient arrangement of this subject will consist in first studying the mucous membrane of the branchiæ of fishes; 2nd. the blood-system; and 3rd. the supporting frame-work.

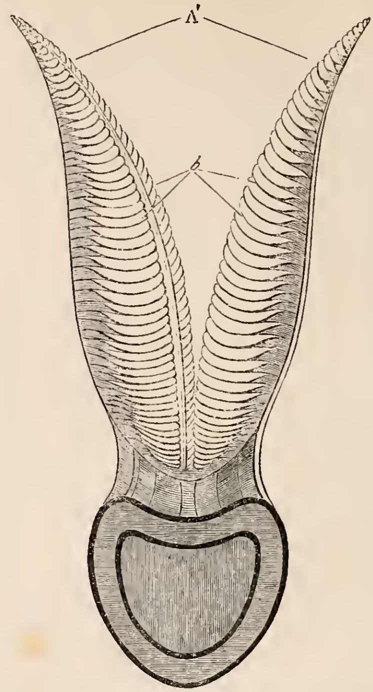
Mucous membrane of the branchiæ. — The gills of fishes are lubricated and defended by a glary viscid secretion: this is the product of the epithelium. This latter, therefore, even on these parts enacts a secernent office. On the plane superficies of the leaflets, the epithelium constitutes a single stratum, resting immediately on the expanse of the *rete mirabile.* In this situation, as in all others, the epithelial layer is supported by a limitary membrane. From its extreme attenuation, however, it does not easily admit of separate definition. Neither cytoblasts, granules, or any other immature particles, mingle with or underlie this layer of *adult* epithelium. It is difficult to conceive the mechanism of their renewal. In the interior of its component cells, however, the eye clearly distinguishes a nucleus and a few pellucid granules. It has already been proved that these latter parts are almost suppressed in the epithelium which lines the active capillary segments of the true lung. Of the branchial epithelium of fishes it may be said that it unites the glandular to the mechanical function of the pulmonary epithelium, that its office is exclusively mechanical. The *halitus* of the air-cells is not a *secreted* product. It is a transpiration.

Viewed with reference to the principles of exosmoses, a layer of amorphous granules, the cytoblasts of future epithelia, interposed between the blood-vessels and the superficial strata of adult cells, would obviously render the partition to be traversed by the gases engaged in respiration very inconveniently dense. The structure presented by the epithelium of the branchiæ implies, that in the organs of aquatic respiration the blood is brought less directly into relation with the external medium than in those of atmospheric breathing. The cells investing the branchial capillaries are not structureless, hyaline, flattened scales, devoid of nucleus and granules, as though the principle aimed at were merely the mechanical one of *thinning* to the extremest practicable limit all structures between the blood and the outer medium. They constitute irregularly oval bodies, carrying a nucleus, and provided with a few pellucid molecules. No cilia exist in the gills of fishes. In their fixed condition, as in the cyprinoid families, in their concealed situation, as in the shark tribe, or their exposed and free position, as exhibited in the higher osseous orders,—forms enough diversified, these organs are characterised alike by the complete and uniform absence of vibratile epithelium.

The Vascular System of the Branchiæ. — In fishes, the whole force of the heart and bulbous aorta is expended upon the branchial circulation. The power of the heart is materially reinforced by the resilient structure which composes the parietes of the aortic bulb. This structure is remarkably contractile. By all standard authorities on comparative anatomy the muscular nature of the walls of the bulbous aorta is admitted without question. The interior of this "bulb" is strengthened by *carniæ columnæ.* It is a fact of no common interest that the colour of the muscular structure of the ventricle is higher or redder in ground-fishes than in those species of which the habitat is superficial in the water, and which are gifted with the power of active locomotion. These facts are indicative respectively of superior and inferior degrees of muscular irritability, and well shown to conspire with other proofs to determine a difference in amount between the respiration of deep and surface-swimming fishes. The valves which guard the proximal and distal portions of the *bulbus arteriosus* vary in situation, number and size, in different families. The movement of contraction which takes place in this vessel is not instantaneous in duration, like that of the ventricle: it is slow and vermicular. The pressure which is thus exerted upon the column of the blood is continuous. The near proximity of the delicate capillary structures of the branchiæ to these powerful centres of force, demands the graduated manner in which the aorta reacts upon the stream of the blood. This mode of action also explains the purposes subserved by the "valves," which in some instances occupy an advanced situation in the vessel. The abdominal aorta, which results from the confluence of the branchial veins, differs considerably in structure from the pre-branchial division of the vessel: the parietes of the former resemble those of a vein. *No pulsations* are detectible in the abdominal aorta of fishes. The pulsatile movement of the blood, derived from the systole of the ventricle, ceases at the branchial capillaries. In fish, therefore, arterial pulsations exist in no other part of the circulating system than in that limited segment which intervenes between the branchial network and the cardiac ventricle. Neither the head nor any other part of the body receives blood *directly* from the cardiac ventricle. The carotids, the homologues of the subclavian, the hyo-opercular and orbito-nasal arteries proceed from the abdominal aorta at the point of confluence of the branchial veins. In these vessels, therefore, the blood is arterialised, while its movement is impulsatile or venous. The propulsive agents, under the form of diminutive lymphatic hearts, which Dr. M. Hall*, M. Fohman†, and J. Müller‡ have shown to guard the several points of communication between the absorbent and venous systems, probably renders as great assistance in circulating the contents of the latter as those of the former orders of vessels. In the whitebait (*Clupea alba* of Yarrell) these microscopic hearts can be most perfectly observed. From a consideration of the preceding traits distinctive of the circulation of fishes, it will be afterwards shown that the laws of aquatic respiration are destined to receive new elucidation.

Minute Circulation of the Branchiæ. — The branchial arteries proceed on either side, symmetrically, from the aorta, and travel through a groove along the convex border of the branchial arches, the veins lying to the outside of the artery, that is, *next* to the pectinated fringes of the gills. The cartilage system of the arches and that of the penknife-shaped processes (bearing the ultimate bronchial leaflets) are quite distinct and unconnected save by fibrous structure. It is in the intervals between these solid parts that the trunks of the vessels are disposed. As the pectinated processes (*a*, *fig.* 235.) arise, when biserial, alternately from the arch, the arterial branches leading to them observe a similar arrangement. The arteries carrying venous blood invariably run along the thick border or outer margin of each process, the vein occupying the innermost edge. A branchial process, attached at right angles to the convex border of the arch, resembles a penknife, the back of which corresponds with the thick and outermost borders, and the *edge* of the blade with the thin or acute side of the process. A string carried from base to point would mark the position of the branchial artery conveying venous blood: brought back along the acute edge, it would denote the line of the branchial vein bearing arterial blood. In the marsupio-branchii (as the myxine, lamprey, &c.), in which the gills are fixed and inoperculate, this is also the virtual arrangement of the secondary trunks. In the lophobranchii (sea-horse, pipe-fish, &c.), in which the branchiæ are tufted, the disposition of the minute vessels is not dissimilar. The *flat* surfaces of the penknife-shaped process are gorgeously festooned by foliaceous multiplications of the membrane (*fig.* 235, *b*). In the annexed illustration, *one* of these leaflets has been shown. In length it does not coincide with the width of the process; the secondary trunks, passing through the substance of the

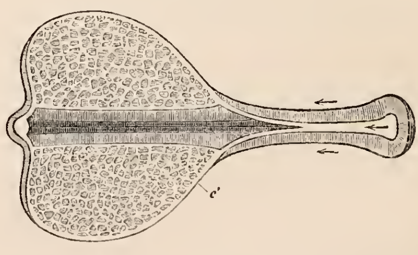
Fig. 235.



A. *Two lamellæ or penknife-shaped processes of the branchial arch of the Cod-fish.* (*Original.*)
b, the vascular respiratory plicæ, which extend only three-fourths across the flat surface of the process. They are seated on the internal longitudinal half or edge of the penknife-shaped process.

cartilage (*b*) at right angles with the primary (*a*) are longer than the corresponding secondary veins on the opposite side of the bladelet; hence the one-sided position of the

Fig. 236.



Represents a transverse section of one of the penknife-shaped processes (with a single leaf bearing the ultimate respiratory capillaries on each side); the web of vessels forms a single *layer. and is covered by a pavement epithelium.* (*Original.*)
c denotes the elastic chord which runs along the circumferential border of the leaflet.

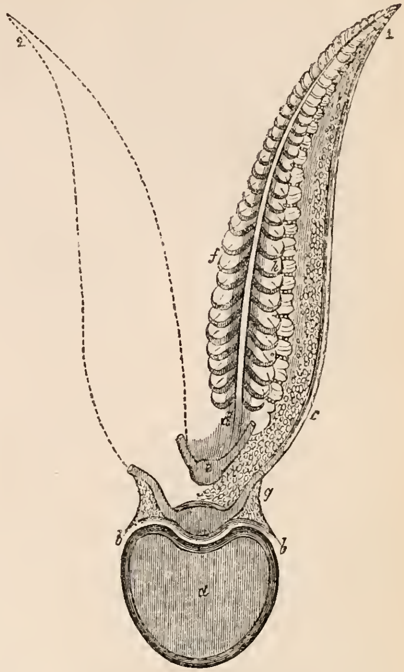
leaflet (*c*) bearing the *capillary network*. These membranous processes, by which the active breathing surface is so extensively multiplied,

* Essay on the Circulation of the Blood.
† Sangader system der Wirbelthiere. 1827.
‡ Elements of Physiology, by Dr. Baly, 2nd ed. Lond. 1839.

are placed, like the leaves of a book, in close apposition with each other, the unattached sides floating freely in the water, the current of which, as it traverses the branchial passages, bearing directly on the flat surfaces or the leaflets, separates them effectually from each other. Viewed edgewise, as represented in the following sketch, the arrangement of these respiratory membranous extensions may be more fully understood. On the branchial processes of the eel these leaflets amount to 700 in number; on those of the turbot, to 900; on those of the cod, to 1000; on those of the salmon, to 1400. Especial attention is invited to *fig.* 237. It shows that *only* the mucous membrane (*i. e.* the layer of epithelium and basement membrane) is *doubled* upon itself, so as to assume the form of folds, *the stratum of capillary blood being single.* From this beautiful arrangement it results that the blood, in its passage through the labyrinth of this plexus, must present *two* sides of an extremely divided stream to the agency of the circumfluent medium. If the network of vessels were duplicated upon a supporting basis, only one side of the sheet of blood could receive the influence of the surrounding medium. Regarded mechanically, such a plan would present little of the delicacy and perfection which really distinguishes this most elaborate specimen of organised structure. This *single*-layer disposition of the respiratory vessels, doubling thus the surface of exposure, obtains as the universally prevailing type of structure in the breathing organs of aquatic animals. It is an arrangement which facilitates in a very remarkable manner the interchange of gases between the blood and the water. The capillary vessels of the branchiæ of fishes, in internal diameter, exceed very little the long axis of the blood-corpuscle. The internal calibre of these channels varies from $\frac{1}{900}$ to $\frac{1}{700}$ of an inch; the blood-corpuscle in the cod measure in the long diameter $\frac{1}{1547}$ inch, and the channels forming the capillary network present in all parts precisely the same calibre.

Cartilage, or Supporting System of the Branchiæ. — The skeletons of fishes are structurally distinguishable into three classes; the osseous, fibro-cartilaginous, and true cartilaginous. In the conventional language of comparative anatomists the last is described as the least completely organised, and the first the most. This distinction, however, which obtains in the adopted nomenclature of science, has no counterpart in that portion of the skeleton which sustains the foliage of the branchiæ. In the *petromyzon fluviatilis* the wicker-work of cartilage which Müller has called the cartilaginous basket of the branchiæ, and which Prof. Owen regards as homologous with the epibranchial system of osseous fishes, detaches processes of almost membranous tenuity stretching inwards to supply a mechanical support to the slender respiratory foliage. In the myxinoid families, cartilage and calcigerous structures are substituted, in various parts of the body, by elastic fibres. In the osseous fishes the

Fig. 237.



Skeletal framework of the lamellæ of the gills in Fishes (*Original.*)

a, section of the branchial arch, which, in osseous fishes, consists of well-marked bone, and in the cartilaginous, of soft cartilage; *b*, marks the junction between the system of the arch and that of the lamellæ, proving that the latter is quite distinct from the former; *c*, illustrates that portion of the framework which occupies the obtuse border of the lamella, exhibiting its external thick marginal fluted channel destined to convey the branchial *artery* from the base to the apex of the lamellæ *d*, denotes that part of the skeletal fabric which coincides in situation with the acute margin of the lamella; *e*, marks the situation of the branchial *vein* as it emerges from the innermost aspect of the axis supporting the lateral processes *f*, which, by their elasticity, keep open or stretched the true membranous respiratory leaflets.

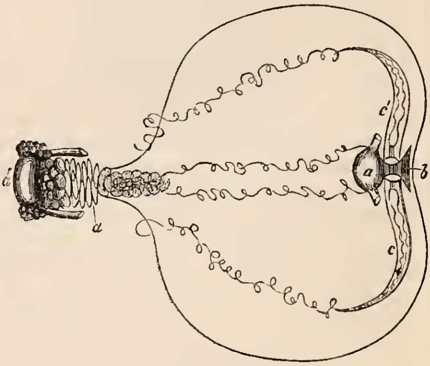
branchial skeleton presents itself under the most readily distinguishable characters. From this class, accordingly, the following illustrative details will be drawn. The respiratory segment of the skeleton comprises the hyoid system and its dependencies, in which are included the branchiostegal rays and the branchial arches, on which, finally, is elaborated an exquisite arrangement of solid points upon which important mechanical functions devolve, in the movements of the apparatus of respiration.* The

* As it is the design of this paper to refer no more to the descriptive departments of comparative anatomy than is found indispensable to elucidate questions of ultimate structure, I must refer the reader, for the solution of the homological and teleological details on this subject, to the work of Prof.

gill-bearing arches are not composed of single undivided curved bones, but of several elements, adjusted with express reference to the elasticity and flexibility of the whole. Six of these arches are primarily developed, and five permanently retained. The first four support gills, the fifth is beset with teeth which guard the opening of the gullet: this latter is termed the pharyngeal arch; the rest the branchial arches. From the convex side of the branchial arches a double series of interlocking penknife-shaped processes radiate. On the flat surfaces of these processes a gorgeous arrangement of membranous leaflets is disposed in a transverse manner, each leaflet standing, as already described, on its edge (*fig.* 237.). This rich foliage, bearing the complex web of the respiratory capillaries, is itself sustained by a machinery of elastic solid parts, hitherto unknown in comparative anatomy.

The series of curvilinear bones denominated the arches of the branchiæ, and exhibited in section at *a*, *fig* 237., are inferiorly attached to the sternal chain of bones, proceeding upwards and backwards, and describing a curve, which in different genera varies in degrees of sharpness, and which finally affix themselves by means of ligaments to the base of the cranial bones. These curved bones are constructed of several separable pieces, adjusted with artful reference to the resilient properties of the curvilinear figure. The act of opening the mouth in the fish determines a consecutive series of movements, which end in the preparation of the gills to be traversed by the branchial current. By an appropriate intervening mechanism the movements of protruding and retracting the mouth occasion irrespectively the approximation and separation of the branchial processes, accompanied by an alternate increase and decrease of the curvature of the sustaining arch. The straight penknife-shaped processes (1, 2. *fig.* 239. *x.*), as stated, diverge from the convexities of the branchial arches. In nearly all the osseous fishes, these processes form a double series, the gills being accordingly distinguished as *biserial*. In those genera in which these processes form a single line the gills are said to be *uniserial*. In the genera *cottus* (bull-heads), *labroidæ* (rock-fish or wrasses), sebastes, (Norway haddock), scorpænidæ (hog-fish), Teidæ (John Dory, &c.), the nilotic-fishes, *polipterus*, gobroidæ (blennies and gobies), *lepadogastidæ*, a genus of small sucker-fishes), and the cyclopteridæ or lump-fishes, may be ranged under one great group, characterised by *three* biserial and one *uniserial* gill. The genera sophiidæ (angler), batrachoidæ, the tetraodons (or globe-fish), the diodons (commonly called the sea porcupines), and that curious genus of monopterus found on the seas of the Mollucas, the gill opening in which is united by transverse partitions of membrane, are characterised by *three* symmetrical *biserial* gills. Other less regular genera present other diversities in the disposition of the branchial processes * The penknife-shaped processes (*fig.* 237.), which radiate from the convexities of the branchial arches are bony in the osseous fishes; but only that part of the solid basis of the process is bony which corresponds with and forms the substance of its blunt or thick margin. In the cartilaginous orders this portion is composed of cartilage, the component cells as well as the outline of which are very dissimilar to those of the former class. As indicated in the above illustration, that piece in the skeleton of the branchial process which forms the obtuse border exhibits a groove seen sectionally at (*b*, *b*, *fig.* 237.), serving for the lodgement of the processal branch (*g*) of the branchial artery. The internal edge of this bony piece is dentated by projecting spines, adapted perfectly to support

Fig. 238.



Plan exhibiting the skeletal framework of the lamellæ of the gills of Fish in transverse section. (*Original.*)

a, shows the osseo-cartilage of the obtuse margin of the lamella, presenting three distinct varieties of component cells, and on the external edge opening into a groove for the lodgment of the branchial artery *a'*, from which, on either side, the ultimate ramusculi, emptying themselves into the *rete mirabile* of the leaflets, may be seen to proceed; *b* and *c*, *c'*, define the beautiful framework which lies parallel with the acute border of the lamella, the lateral processes *c*, *c'* stretching on either side along the circumference of the membranous leaflets, preventing, by their continuously acting elasticity, the injurious folding of the latter, and, therefore, the tangling of the respiratory web of capillaries. The extremities of these processes are produced by means of the curled elastic fibres shown in the plan. The dotted lines define the area of the respiratory membranous leaflets supporting the capillary network.

Owen on Fishes: Rymer Jones's Animal Kingdom; Article Pisces, in this work, by Prof. R. Jones; Art. Skeleton, by Mr. Maclise. I wish only here to observe, that the branchial arches appertain to the apparatus of the visceral skeleton, and in antero-posterior order succeed the hyoid arch, on the keystone of which they are more or less dependant, and the altered configuration of which they more or less follow.

* See Yarrel on British Fishes; Leçons d'Anatomie Comparée, par M. Cuvier; Owen's Lectures on Comparative Anatomy, vol. ii.; Monro, on the Structure and Physiology of Fishes, 1785; Art. Pisces, in this Cyclopædia; Wagner's Anatomy of Vertebrated Animals, by Tulk, 1845.

the soft structures. This part is represented transversely in *fig.* 238, in which also the disposition of the constituent cells may be remarked to bear advantageously upon the mechanical functions of the parts. As regards the arrangement of these cells, this piece in the framework of the gill-process may be divided into two parts, by a longitudinal line, on the outer side of which the long axes of the cells, which are oblong, are directed transversely with respect to the inner: the axes of the cells are parallel with that of the processes of which they are the constituents parts. This arrangement is most distinctly marked in those genera in which the skeleton is little calcified. Functionally considered the piece occupying the blunt edge of the process determines its penknife-like contour, and confers strength and straightness of direction, thus favouring the contact between the respiratory foliage and the surrounding medium. It discharges the passive office of sustaining the soft structures and of extending the plane superficies over which the branchial blood-vessels are distributed.

The internal or acute margin of the branchial process conceals, in the recent structures, under the labyrinth of the superimposed respiratory membrane, a skeletal mechanism of singular novelty and beauty (*f*, *fig.* 238.) From the innermost side (near its root) of the denser piece which lies parallel with the outer margin of the lamella, a less dense, more transparent, and more cartilage-like process (*d*, *fig.* 238.) rises, to advance along the internal margin of the lamella from its base to its extreme apex. From either side of this process, at right angles, processes (*f* and *c c*), still more slender, delicate, and transparent, are detached, to follow for some distance the circumference or free margin of the membranous leaflet on which the vascular network is outspread.

This part of the skeletal fabric of the branchial lamella is *actively* and importantly concerned in the mechanism of the respiratory function. It is to the branchiæ what the ribs are to the mammalian lungs. The fine extremities of these transverse portions, as seen in *c*, *c*, taper off into a species of curly fibre, which *travels accurately along the extreme margin* of the membranous leaflets to the point (*a*) at which the latter rest upon the flat surface of the osseo-cartilage of the obtuse margin. The axis which supports this system of elastic "*ribs*" (in section at *c* and *d*) exhibits under the microscope a median transverse line apparently filled with an oleaginous fluid, which communicates with the moniliform system of cells, occupying the axes of the curved pieces (*c*, *c*), where probably it performs the two-fold office of mechanically distending and nourishing the parts. No vestige of an Haversian order of canals can be discovered in any portion of this branchial framework. The calcareous granules of Tomes are distributed irregularly over the parietes of the cartilage cells. It is not easy to misapprehend the office which devolves upon this apparatus. By means of two needles the recent branchial ray may be separated into two longitudinal halves, to the inner of which, exclusively, the *membranous* leaflets remain adherent, a circumstance which illustrates the anatomical connection between these softer parts and the delicately adjusted framework of the internal border of the leaflet. The elastic transverse processes (*c*, *c*), from their constrained curved position, constantly tend to straighten themselves, and to convert the curved into a direct line of action. This straightening tendency, which is a constantly and unremittently operating force, constitute the immediate agency under which the tangling, folding, or crumpling of the leaflets bearing the capillary network is rendered impossible. Under the ceaseless operation of this resilient property, the true breathing surface is regularly maintained in a state of uniform extension, and that at a degree of lightness, measured with wonderful precision, to suit the exigencies of structures so surpassingly refined. A superficial consideration indeed might have sufficed to render it improbable, that a system of blood-channels of such extreme delicacy as that which constitutes the breathing apparatus of fishes could exist uninjured, unless by aid of a basis of support at once appropriate in its physical qualities and mechanical disposition.

Morbid anatomy of the lungs and air passages. — It is possible in the space here allowed to do little more than to enumerate the pathological conditions to which these parts are liable. The diseases of the lungs and bronchi since the era of Laennec have received a considerable share of the attention of pathologists. The normal anatomy of the lungs is now known with precision. The characteristics of the alterations of structure which in disease they undergo, within recent years have also been defined with corresponding precision. The community between the bronchial and pulmonary circulation established by the recent researches of Dr. Heale, will probably oblige pathologists to modify their views with respect to the supposed distinctness and independence of the diseases of the lungs and the bronchi. The following tabulated arrangement, as given by Rokitansky, in the 4th vol. of his Pathological Anatomy, exhibits the abnormal conditions of these parts in lucid summary.

1. Deficiency and excess of formation.
2. Deviations in size.
    - *a.* Morbid dilatations of the air passages.
    - *b.* Dilatations of the larynx and of the trachea.
    - *c.* Dilatation of the bronchi.
    - *d.* Contraction of the air passages.
    - *e.* Hypertrophy and Atrophy.
3. Deviations in form.
4. Deviations in position.
5. Interruptions of continuity.
6. Diseases of texture.
    - A. Diseases of the mucous membrane and of the subjacent areolar tissue.
        - *a.* Hyperæmia and Anæmia.
        - *b.* Inflammations of the mucous membrane.

1. Catarrhal inflammation.
   a. Acute.
   b. Chronic.
2. Exudative processes (croupous inflammation.)
3. Pustular inflammation.
4. The typhous process on the mucous membrane of the air passages.

c. Inflammation of the submucous areolar tissue.
d. Ulcerous processes.
e. Œdema of the mucous membrane of the air passages.
f. Gangrene of the air passages.
g. Adventitious products.

B. Diseases of the cartilaginous skeleton of the air passages
a. Inflammation of the perichondrium of the laryngeal cartilages.
b. Inflammation and softening of the epiglottis.
c. Ossification.
d. Adventitious products.

7. Anomalies in the contents of the air passages.

Abnormal Conditions of the Lungs.

1. Deficiency and excess of formation.
2. Anomalies of size.—Hypertrophy and Atrophy.
3. Anomalies in form and position.
4. Diseases of texture.
   a. Rarefaction of the pulmonary tissue (Emphysema.)
   b. Condensation of the pulmonary tissue.
   c. Hypæremia (stasis). Apoplexy of the lungs.
   d. Anæmia of the lungs.
   e. Œdema of the lungs.
   f. Inflammation of the lungs (Pneumonia).
      1. Croupous pneumonia, typhous pneumonia.
      2. Catarrhal pneumonia.
      3. Inflammation of the interstitial tissue of the lungs (Interstitial pneumonia).
   g. Deposits in the lungs (Melastatic processes).
   h. Gangrene of the lungs.
   i. Softening.
   k. Adventitious products.

The preceding distribution of the morbid conditions of the air passages may be advantageously methodised under two heads: first, those of the bronchi (as defined in the account of their normal anatomy); secondly, those of the lungs.

The bronchi are liable to several forms of inflammation:

a. Acute bronchitis.
b. Chronic bronchitis.
c. Plastic bronchitis.

Collapse of the lungs should be considered, pathologically, as rightly ranking under the denomination of the diseases of the *bronchi.*

The various forms of *asthma*, and *hooping cough*, belong to this species.*

The bronchi are subject to two forms of *dilatation.* In the *first*, a tube is uniformly dilated at every part of its circumference. In the *second*, the dilatation is *saccular.* The small bronchi and those near the surfaces and borders of the lungs are most liable to suffer this change. The walls of the tubes at the dilatations are hypertrophied and thickened. Sometimes, with the saccular variety, the same parts are relaxed and attenuated.

The *bronchitic collapse* of the lungs occurs under two distinct aspects, the diffused form, and the limited or *lobular* form. Of these the latter variety is the more striking or characteristic, and has been, especially in the lungs of children, the subject of more discussion than the former. But the diffused form is by far the more common, and is of frequent occurrence in its slighter degrees. In both conditions the pulmonary tissue presents a dark violet colour as seen beneath the pleura; internally it is red.

In considering the causes which tend to produce this condition they seem to resolve themselves into the following: 1st. the existence of mucus in the bronchi, which is more liable to produce obstruction according as it is more thick and viscid; and 2ndly, weakness or inefficiency of the respiratory power; 3rdly inability to cough and expectorate. Of these conditions, the first must be considered as the exciting cause, the others as predisposing, co-operating with the first, but incapable, without it, of producing collapse.*

With bronchitic collapse of the lung is almost always associated *emphysema* of the unaffected portions of the same lung (Gairdner).

Inflammation of the mucous membrane of the bronchi produces changes which are denoted by redness and tumidity of the tissue, a secretion of muco-serum, purulent mucus, or pus, according to the stage and intensity of the inflammation.

This latter is the condition of *superficial suppuration.* The swelling of the mucous membrane and sub-mucous tissue, which assumes the form of watery infiltration into the

* For an account of the morbid statis of the larynx, and upper part of the trachea, see Art. Larynx.

* For a full discussion of this interesting subject, see "Pathological Anatomy of Bronchitis, and the Diseases of the Lung connected with Bronchial Obstruction." By W. T. Gairdner, Edin. 1850. Mémoire sur une Distinction nouvelle de deux Formes de la Bronchite; précédé de quelques considerations générales sur l'inflammation de la membrane muquese des voies-aeriennes. Par J. H. S. Beau. Archives Générales de la Médicine, Sept. et Oct. 1848. Mémoire sur quelques Parties de l'Histoire de la Bronchite et de la Broncho-pneumonie chez les Enfants. (Archives Générales, Oct. 1851, et suivantes.) Mémoire sur la Broncho-pneumonie Vesiculaire chez les Enfants. (Révue Médico-Chirurgicale de Paris, 1852. Par les Drs. Barthez et Rilliet.) Traité Pratique des Maladies des Nouveaux-Nes, &c. Paris, 1852. Par M. Bouchut. A Memoir by Legendre and Bailly, in the Archives Générales de Medicin, on the "état fœtal" of the lungs, tom. lxiv. On the Diseases of the Organs of Circulation and Respiration, Art. Atelectasis. By Hasse. Sydenham Society. Die Bronchio-pneumonie der Neu-gebornen und Säuglinge. Berlin, 1837. By Seifert. Medico-chirurgical Trans., for 1830. By Dr. Alderson. Der Mechanismus der Respiration und Circulation. By Mendelssohn. Beiträge zur Experimentellen Pathologie und Physiologie. By M. Traube. Die Bronchitis der Kinder. Leipzig, 1849. Dr. Fuchs. Diseases of Infancy and Childhood. West.

areolar tissue, being accumulated at individual spots, is important and worthy of great attention, on account of the facility with which it interferes with the calibre of the tubes.

Chronic inflammation of the bronchial membrane gives rise, especially in parts abounding in glands, to *glandular hypertrophy*, *mucous polypi*, *epithelial growths*, *spongy* and *velvety* thickening, *relaxation* of the muscular and fibrous elements, *follicular ulceration*, &c.

The pathological conditions of the broncho-pulmonary mucous membrane differ in no respect from those of any other membrane of this class.

In *plastic* or *exudative bronchitis* are characterised by a morbid action of a *croupous* nature.

In *bronchial croup* the tubular exudations from the larger bronchi present a calibre inversely proportional to their thickness, and those thrown off from the finer ramifications occur as solid cylinders.

Asthmatic affections may either have their exciting cause in the lungs or in the condition of some remote organ. They partake of a nervous and muscular character, and are frequently caused by a *collapse* of a portion of the lung. The collapsed part operates as an excitor of the muscular spasm.

English pathologists recognise the following forms of disease proper to the parenchyma of the lungs: — *Pneumonia*, or inflammation of the cell-tissue of the organ; *gangrene; hæmorrhage; œdema; emphysema; phthisis; cancer*.

Inflammation of the vesicular tissue of the lungs is marked by the exudation of the coloured elements of the blood. This fact was once supposed to prove the absence of epithelium in the air-cells. This inference is erroneous.

Inflammation of the lung is divided into *three* stages, according to the consistency or physical condition of the exuded product. The first is that of *engorgement*; the second is that of *hepatisation*; the third is that of *grey hepatisation*.

Gangrene of the lungs occurs under *two* anatomical forms, the diffused and the circumscribed.

Cancer of the lung, most commonly of the encephaloid species, occurs in the forms of secondary nodules and primary infiltration, accompanied or not by tuberous formation on either mediastinum about the main right bronchus (Walsh).

The anatomical changes which occur in the lungs in phthisis are referrible to three main stages, corresponding habitually to certain varieties in the symptoms, and always to modifications in the physical signs. The first stage is that of *deposition* and *induration;* the second that of *softening;* the third that of *excavation*.

The exact *seat* of pulmonary tubercle has proved, from the dawn of pathology to the present time, a controverted point. The question is whether the deposit of the morbid product occurs first on the free surface of the air-vessels into the substance of their walls, or *between* them into a supposed intervesicular tissue. From Morton and Bayle to Rokitansky and Lebert, advocates for each of these "seats of election" have contended in turn. The free or aerial surface of the air-cells is now the commonly accepted situation of the tuberculous deposit.

The *nature* of the tuberculous matter is not less disputed; witness the following definitions: —

Tubercle is a *specific* exudation (Ancell).

Tubercle is a degraded condition of the nutritive material (Dr. C. J. B. Williams).

Tubercle is composed of the products of inflammation (Reinhardt).

Tubercle is composed of the dead-tissue elements (Henle).

Tubercles themselves consist of *abnormal* epithelial cells (Dr. W. Addison).

Tubercles are composed of metamorphosed organised elements; a metamorphosis co-ordinate with the fatty and the waxy degenerations (Virchow).

Tubercle is a product *secreted* from the blood by the *epithelium* lining the air-cells (Schroeder Van der Kolk*).

The *mechanism* of emphysema is still *sub judice*. Some authors, with Laennec, explain it on the supposition that the walls of the air-vesicles *yield* under the force of the air when the *expiratory* current is impeded. Another class of writers attribute it to an excess in the inspiratory force. Mr. Rainey contends that the parietes of the air-cells suffer a change of structure by fatty degeneration, and that this change stands to emphysema in the relation of a causal condition. Dr. Gairdner affirms that emphysema of one portion of the lung *cannot* occur unless a *collapse* has happened in another part. Emphysema fills up pneumatically the space lost by the collapse, and no more. The chest can only be *filled;* it cannot be inflated beyond a given inspiratory limit. The air-passages of the emphysematous portions are *free*, not obstructed. If already the cavity of the thorax be *uniformly* filled, it is certain that emphysema is rendered physically impossible. Emphysema is *plenum* counterbalancing collapse — a *vacuum*.

It is yet by no means determined to what extent, if at all, the shedding or desquamation of the *epithelium* of the air-passages takes place in disease.

(*Thomas Williams.*)

STOMACH AND INTESTINE.— (Syn. *Stomach*, formerly *Maw*, Eng.; *Magen*, Germ.; στομάχος, γαστὴρ, Gr.; *Stomachus*, *Ventriculus*, Lat.; *Stomaco*, *Ventricolo*, Ital.; *Estomac*, Fr.; *Estomaco*, Sp.; — *Intestine* or *bowel*, formerly *gut*, *tripe*, *entrail*, Eng.; *Darm.*,

* See British For. Med. Chir. Rev., for January April, July, 1853; in which Nos. respectively three excellent articles by Paget, Jenner, and Sieveking, will be found.

Germ.; ἔντερον, Gr.; *Intestinum*, Lat.; *Intestino*, Ital. Sp.; *Intestin*, Fr.*)

What are called the organs of the animal body consist of a diversity of tissues, so grouped and united with each other as to form a more or less continuous and aggregate mass;—the functions of these various structures being also associated in a single general purpose, which may be regarded as the sum of their several actions on the system at large.

Among such groups of structures, there is none more remarkable than that which effectuates the series of processes collectively termed Digestion. For other organs are so far exclusively dependent on the blood, as that many influences of the outer world can scarcely reach them, except through the medium of this fluid. Entrenched, as it were, behind this the great river of animal life, they are secured from any but the indirect action of numerous physical agents. But the organ of digestion lies outside this stream: and occupies a kind of neutral territory, between life and matter, where the various forces of both can cooperate for its benefit, in equal and harmonious conjunction. Or rather, let us say, the digestive canal is the threshold of the House of Life, where dead matter is first endowed with those properties which enable it to become a living constituent of the animal body.

The group of organs before us has indeed a special relation to the animal. For although digestion is usually enumerated amongst those general or organic functions which are shared in by everything that has life,—vegetable as well as animal,—still the means by which the process is effected in these two forms of organization, constitute as important a distinction between them, as the mere presence or absence of other functions. So that, the digestive cavity is, on the whole, as characteristic of the animal, as the organs of locomotion and innervation of which it is the exclusive possessor.

How far the so-called vegetative functions are really alike, or even comparable to each other, in the two kingdoms of nature, it is not our object here to inquire. As little do we wish to introduce, what some might perhaps think less out of place, a detailed comparison between the digestive functions of the plant and animal. But as the cavity which it is our express object to describe is all but universally present in the latter, and absent from the former organization, it seems desirable briefly to contrast them in this respect.

In the animal, a highly azotized composition is connected with,—and probably essential to,—an active life; which, in its turn, implies a rapid waste of substance. On the other hand, the plant lives slowly, wastes little, and contains but a small quantity of azotized material.

The food of each appears to correspond with these requirements. That of the plant is, in great part, inorganic; consisting mainly of compounds which pervade the soil that surrounds its roots, or the air which bathes its leaves. While that of the animal is organic:—*i. e.* the substances which compose it are the products of a previous organization.

The elaboration of the food repeats the preceding contrast. The plant builds up inorganic into organic matter;—a process of chemical synthesis, which may well be effected with great difficulty, and by slow stages. While the animal scarcely does more than convert one proximate principle into another;—a metamorphosis which involves no change of composition, and the facility of which is but partially counterbalanced by its requisite rapidity and amount, and the delicacy of its adjustment.

The agents of these processes are also susceptible of comparison. For in the vegetable they appear to be closely connected with various external forces, such as light and heat; while in the animal they seem more inherent to the organism.*

And in both, the site of the elaboration or change in the food corresponds to those situations where the above agents are most readily applicable:—viz. in the plant, to the leaves and other green parts of its surface; in the animal, to a cavity in its interior. The presence of such a cavity not only permits the less frequent application of nutritious substance to be compensated by the ingestion of large quantities at particular times; but, while it thus meets the peculiar requirements of an animal organism, also allows of that locomotion which is so necessary to the mere prehension and selection of its scarcer food. Its subjection to volition renders ingestion a work of rapid and powerful mechanical force, in place of a slow physical imbibition. And finally, the same internal situation which directly subjects its contents to the agents of the digestive metamorphosis, also isolates them from all surrounding objects, besides favouring the temperature often necessary to the operation.†

* In respect to the etymology of these names we may conjecture as follows:—The word γαστὴρ is radical. The *stomach* is so called from its connection with the mouth (στόμα). *Maw* and *magen* are derived from its relation to food (*meat*). *Intestine*, ἔντερον, *entrail*, *ventriculus*, (and *darm?*) connote its internal and hidden position. *Bowel* (*botellus*), and *tripe* (τρέπειν), refer to its convoluted or tortuous form: *gut* (*geotan*, Anglo-Saxon, to pour), to its carrying fluent contents.

* Traces of this contrast between the animal and plant during life may be found in those processes of putrefaction and eremacausis which respectively effect their dissolution after death.

† Hence, instead of a digestion corresponding to that of the animal, the plant presents us with a process in which mere reception is so predominant, that we might almost compare it with the absorption of the chyme and chyle into the blood. As a kind of fanciful corollary to this, we might regard the crust of the earth, and the atmosphere which surrounds it, as forming a common stomach or receptacle of food for the whole vegetable kingdom. For they include, or receive, detain, and give up, the chemical food of the plant;—in quantities which, though

The reader will, however, observe, that the title of the following article does not announce an essay on the process of digestion, or the various organs which effect it; but limits itself to two portions of the alimentary canal, hitherto undescribed in this work. But it is impossible to treat of the functions of the stomach and intestine except in connection with the entire process in which they take so large a share. While the numerous observations and researches which have been made since the appearance of the earlier article DIGESTION require some notice in the *Supplement* of which the present essay forms a part. For these reasons the author has felt it advisable not to confine himself too strictly to the exact limits which the heading "Stomach and Intestine" might seem to imply. Hence, though the following essay will treat chiefly of the above segments of the alimentary canal, it will also comprise a very brief account of whatever is at present known concerning the whole digestive act. Commencing by a rough sketch of the anatomy of these parts in the animal kingdom, we shall successively consider, their structure and functions in the human subject; their relation to digestion and nutrition; and finally, their appearances in disease.

COMPARATIVE ANATOMY.—In the *Infusoria*, whose minuteness places them at the lowest extremity of the animal kingdom, the organ of digestion has already attained such a development as to form the chief basis of their nomenclature.

One or two genera present us with a rare and exceptional condition:—viz. the absence of all traces of digestive cavity. Such are the parasitic *Gregarina* and *Opalina;* in whom, as in some of the *Entozoa*, digestion and absorption appear reduced to a simple physical process of endosmose, which carries the nutritious substances dissolved in the fluid medium they inhabit at once into the mass of their corporeal juices.

The *Polygastria* possess a plurality of stomachs or internal sacs; and the relations of these to the intestine, together with the condition of the latter tube, subdivide this group into numerous families and genera. Thus many are named "anenterous," because they appear to be devoid of intestine. Of these the *Monas termo*—which has four or five globular stomachs, of $\frac{1}{20000}$th of an inch in diameter, appended immediately to its mouth—may be taken as the type. Others possess similar sacs in connection with a simple Intestine; and are chiefly distinguished by the straight, curved, or wavy course of this canal,—or by the single or double character, and lateral or terminal position, of its apertures. Most of them devour a living prey of kindred Infusoria;—prehension being often visibly effected by cilia, the voluntary action of which carries a current of food into the mouth, or removes egesta by a simple reversal of the stream. And sometimes this act of ingestion is aided by a dental apparatus, in the shape of a hollow cylinder enclosing long teeth,—as in the genus *Napula*.

The *Rotifera* are so named from the currents produced by their prehensile cilia; which are here limited to groups surrounding the mouth of the animal.

Many of them have an organ of mastication. This usually consists of three pieces:—each of the two facets of a kind of anvil being worked upon by the rough or toothed terminal surface of a recurved jaw, the longer limb of which receives a muscle at its extremity.

The intestinal canal generally exhibits a pharyngeal enlargement, which is followed by a narrow "œsophagus," of varying length, ending in a wider "intestine." In the *Gasterodela* a dilatation, called a stomach, precedes the intestine. In the *Rotifer vulgaris* and others, an almost globular enlargement of the narrow canal is so immediately followed by the constricted cloaca, as to have been compared to a large intestine. The organ of digestion is also often complicated by the presence of blind tubes; which vary, not only in number and size, but also in position, and possibly in import. Thus they may open, either into an uniform and narrow canal, or into the commencement of the intestine, or into the presumed gastric dilatation;—or, finally, as in the *Diglæna lacustris*, a set of such tubes may occupy both of these latter situations.

The various members of the order *Entozoa* are grouped together in obedience to a classification which is here and there arbitrary and anomalous, but in the main both natural and useful. It offers three chief varieties of the digestive organ, all of which are very interesting.

α. In many—as in the *Echinococci* and their congeners—no trace of a special digestive cavity is present. Without mouth, stomach, or intestine, the creature floats free in the cavity of its enclosing cyst, or buries its barbed head in the tissues of a living habitation;—whose juices, thus brought into relation with its exterior, are applied to its nourishment by what seems to be rather a process of endosmose than of digestion properly so called.

β. In other genera belonging to the *Cestoid* and *Trematoid* divisions, there is, however, a canal, which is apparently related to digestion, and the main features of which—repetition and ramification—may be represented by the *Tænia* and *Distoma* respectively.

For example, in the Tape-worm, a minute mouth opens into a slender tube, the bifurcations of which reach the margins of the body where this begins to assume its regular jointed form. From hence onwards the canal might be compared to a ladder, with rungs at the fore and aft extremity of each joint, at the right angles of which its longitudinal and transverse branches unite. It is probable that these canals possess valves. But whether they have any constant or valid terminal orifices seems doubtful.

ordinarily sufficient, are capable of being locally exhausted by the excessive demands of a particular class or species, and renewed by an artificial supply.

Many species of *Distoma* or Fluke may be regarded as types of an arborescent or ramified digestive tube. From a mouth which is suctorial—and sometimes visibly muscular—a canal passes backwards, to divide into two large branches. These run along the margins of the oval and flattened animal, giving off other branches; from which proceed a final series of anastomosing twigs.

γ. In many creatures closely allied to the preceding by conformation and habits, this ramified canal is reduced to its primary bifurcations, the ends of which are sometimes slightly dilated. Occasionally there is an enlargement, which has the situation of a pharynx; and which, in a few instances, encloses an apparatus perhaps masticatory. In the genus *Diplostomum* and others, a distinct set of vessels, which occupies the immediate neighbourhood of the intestine, has been supposed to represent a chyliferous or vascular system.

As regards these latter forms of digestive apparatus, it may be conjectured, that the ramification witnessed in the *Tænia* is referrible, not so much to that mere vegetative repetition of similar structures which affects the whole animal, as to a merging of the digestive in the circulatory function. In any case, the more simple form of tube last mentioned appears rather akin to an advance, than to a retreat, of development; while it sometimes visibly coincides with the appearance of a new system of canals, connected with the circulation of a proper nutrient fluid.

In the *Nematoid* Entozoa, the alimentary canal is generally a straight tube, which occupies the axis of the vermiform animal, and opens at its extremities. In most genera — as in the *Trichina*, *Tricocephalus*, *Ascaris*, *Strongylus*, and others — it widens posteriorly; where it often experiences a further dilatation, which only ceases near the anus. Rarely, other indications of separation are added: — an œsophageal dilatation, as in the *Ascaris lumbricoides;* or an enlargement corresponding in position to a stomach, as in the *Linguatula* and *Filaria*.

Rudiments of the organs accessory to digestion have also been detected. Blind tubes opening into the canal near its mouth are found in several genera: and the position of these has sometimes led to their being regarded as salivary. While rarely there is a tube which opens into the intestine in the situation of a biliary organ.

In the mode of attachment of their digestive canal, this division of the *Entozoa* offers a marked contrast with the preceding. In the *Sterelmintha* (or *solid* worms) the tube is scarcely distinguishable from the mass of the body. While in these *Cœlelmintha* (or *hollow* Nematoid worms), it is suspended from the wall of the belly by filamentous processes. And though such an acquisition of an abdominal cavity is no doubt partly referrible to the isolation demanded by the organs of locomotion, yet not only does this itself imply a general advance of development, but it is actually accompanied by a curious structure, which is apparently connected with nutrition, and possibly renders the cavity of the abdomen the receptacle of a kind of chyle. Its more perfect form in the *Ascaris lumbricoides* may be briefly described as consisting of a series of pyriform processes, the peduncles of which are seated immediately upon the mesenteric filaments previously alluded to, and which project freely into the abdominal cavity, so as to be surrounded by the serum and grey transparent substance that fills this space. Their shape resembles that of the villi of higher animals; and their size increases towards the median line of the body.

The alimentary canal of the *Polyp* exhibits so wide a range of development, that while by one extreme it approaches that of the simplest anenterous *Infusoria*, by the other it attains a complexity akin to that of the highest Invertebrata.

The *Hydra* is little more than a stomach or sac, fixed by a sucker at its closed extremity, and having at its other end a mouth surrounded by prehensile tentacles. Digestion is, however, energetic. The living prey, which is paralysed by the deadly grasp of the tentacles, undergoes a rapid solution in this stomach, while its colours often visibly mix with those of the parietes common to the organ and the animal; and finally, its excrementitious residue is speedily rejected by the same orifice through which it previously entered.

In other solitary Polyps—for example in the marine *Actiniæ*—the folded bag formed by the stomach is separated from the mouth by an œsophageal constriction. It is at the same time attached to, and isolated from, the general wall of the animal, by radiating muscular bands; which extend vertically down the whole depth of the organ, so as to resemble the septa of a poppy capsule as seen in a transverse section.

The *compound* Polyp appears chiefly to vary from this type by virtue of its individuals possessing a common stem, the proper nutrition of which requires it to be closely connected with the organ of digestion. Thus, in some of the *Anthozoa* which possess a stomach very similar to that of the Sea-anemones just described, an orifice of small size at the bottom of the gastric sac seems to admit the results of digestion into the general cavity of the animal, within which they experience a kind of circulation.

In the *Tubularian* Polyp, the canal is modified by the addition of a structure which may be regarded as a pharyngeal proboscis. It is a globular projection, surrounded by tentacles at its free extremity, and by its other end received immediately within a circle of similar organs;—the place of its attachment being marked by an internal constriction, through which the cavity of this appendix communicates with that of the stomach.

In many of these Polyps, the stomach has been seen to possess a ciliated lining; and there are grounds for presuming the existence of a similar structure in several other species. Some of the circulatory movements observed in their ingesta are perhaps accomplished by the aid of such an apparatus. While their vigorous and almost peristaltic character in other instances is due to structures, the voluntary and powerful contractions of which entitle them to rank as muscles.

The *cilio-brachiate* Polyp possesses an abdominal cavity occupied by fluid, in which the alimentary canal is free to move. The canal itself has a mouth and anus, which are both situated at the free extremity of the animal;—the former orifice being within, the latter without, its whorl of tentacles. The mouth opens into a pharyngeal dilatation, from which a narrow tube leads into an organ analogous to a gizzard. This organ possesses radiating muscular fibres, and rhomboidal teeth, that are capable of crushing its contents. Immediately beneath it is the stomach, in shape like a two-necked flask, and having its blind extremity fixed to the attached base of the animal by a retractory muscle. The pyloric aperture is guarded by cilia, which rotate, and thus delay, the food. The intestine is narrow and simple, and its excrementitious contents are expelled from the anus, to be immediately hurried away by the current arising from the action of the neighbouring cilia.

The body of the *Acalephæ* generally constitutes a disc with a fringed margin. It is convex above, and concave below, with large dependent processes. And it swims by what seems to be an alternate preponderance of contraction in these two surfaces.

The condition of the alimentary canal is here very remarkable. The Entozoa have already offered us a ramified tube, that could scarcely be regarded as strictly digestive. But these Sea-nettles further complicate this branched state by the possession of a central cavity. This is sometimes placed between a convergent and a divergent set of anastomosing canals; and sometimes approaches the stomach of the Distoma in possessing the latter set only. In the latter case, the so-called stomach communicates, by a short and simple tube, with the centre of the lower or concave surface. And in one species it also radiates unbranched tubes which open on the margin of the disc. The movements of the contents of these canals seem to be effected by cilia. The ramifications of the canals chiefly occupy the under surface of the animal.

The large order of *Echinodermata* again presents us with an important advance of development in passing from its lowest to its highest members.

Thus the alimentary canal of the *Asterias* has a single aperture on the under surface of the animal. This leads by a short tube to a central cavity, which divides into two processes for each ray. These processes give off secondary branches at right angles to themselves, and the latter end in tertiary cæca. In *Comatula* the cæca disappear, and the canal acquires a distinct mouth and anus, which open near each other. In all, the canal is muscular, is enclosed in a ciliated peritoneum, and has its primary divisions attached by a kind of mesentery.

In the *Echinus*, the anus generally opens on the upper or opposite surface of the body. Many of this genus have a complex masticatory organ, which is acted upon by powerful muscles. The first part of the canal opens into an intestine of much larger diameter, opposite to a blind dilatation very like the human cæcum. The intestine is coiled twice around the inner surface of the shell; the second coil reversing the direction taken by the first, and both exhibiting a sinuous course. Its width tapers away to the anus. Its structure is delicate and transparent; it possesses a mucous membrane, and longitudinal and transverse fibres; and it exhibits an intestinal vein, which is especially marked towards the termination of the canal.

In the vermiform *Holothuriæ* the canal forms a kind of Z in the abdominal cavity;—passing first backwards, then forwards, and again backwards to its posterior extremity. The first part is wider and stronger than the rest, and its more glandular mucous membrane presents longitudinal folds which terminate in a slight circular one. Such a structure causes this dilatation to be regarded as a stomach. The narrowing intestine often terminates in a large oval cloaca, into which open two branching cæca.*

The *Annelida* form a class of animals so diverse in nature and structure, that it is difficult to include all the varieties of their digestive apparatus within a mere brief sketch. The canal always possesses a distinct mouth and anus, which occupy the opposite ends of the more or less elongated and cylindrical body. Prehension is generally aided by teeth, which, as in the Leech, perforate the skin of their prey; while in others—as in some of the *Errantes*—it is effected solely by a proboscis. In many of the marine *Errantes* the intestinal canal is simple. In the *Lumbrici* the canal soon dilates into a membranous pouch, which is followed by a thicker and more muscular portion, supposed to be a gizzard. In some genera, this part of the tube is complicated by being produced into pouches. These are either numerous, as in the Leech; or few, as in some kindred genera. Finally, in the Earth-worm, they are reduced to mere constrictions of the canal; while in the *Aphrodita*, they are developed into tubes, which expand, divide, and terminate as almost globular pouches. Clusters of glandular follicles, which are supposed to be biliary, open into the posterior half of the complicated canal of the leech just alluded to: and analogous structures are found in other genera. In the Earth-worm, there is a singular apparatus, the *typhlosole*. This is a blind tube, which occupies almost the whole length of the canal, being attached to its dorsal aspect, and

* Such a complex organization is strangely contrasted with the alleged fact, that the animal, when alarmed, can shed the whole canal. This extraordinary act is presumed to be voluntary, and is only paralleled by the growth of another digestive apparatus, which replaces that evacuated.

projecting into its cavity. Its interior surface is folded and villous. The whole structure appears to be connected with a kind of chylous absorption.

The alimentary canal of the *Epizoa* differs from that of the cavitary *Entozoa*, in being generally surrounded by a glandular mass, the function of which is probably hepatic. The *Cirripeda* have prehensile jaws, and a terminal mouth and anus. In some, the canal has a gastric dilatation. Hepatic follicles, similar to those already described, occur here also. And St. Ange and Serres have found a tube analogous to the typhlosole.

The digestive tube of the *Crustacea* may be reduced to two chief forms, which correspond with other differences in the nature and structure of their possessors. Thus in those lower Crustaceans which are suctorial and parasitic, the canal is a very simple one. A proboscis conceals a pair of lancet teeth, and is followed by a straight intestine, around which are clustered a dense mass of follicles, supposed to constitute a liver. The higher Crustaceans possess a complicated apparatus of forceps and jaws. A short œsophagus leads to a large spherical cavity, which occupies the head of the animal, and which, although sometimes called a stomach, contains hard structures that render it analogous to a gizzard. A well-marked constriction separates this organ from the intestine, which is sometimes simple and nearly straight, sometimes divided into two portions distinguished by a projecting valve. The liver is conglomerate, and divided into lobules. Rarely, one or two cæcal tubes are also present.

The alimentary canal of the *Insect* offers what are rather varieties of development than any regular transition, such as we have remarked in some of the preceding orders:— varieties which the metamorphosis of the larva at present seems to complicate instead of explain.

In the *larva*, the canal is comparatively simple, and somewhat approaches the condition seen in the lower *Annelida*: being a straight tube, with a mouth and anus at opposite ends of the body. In many Hymenopterous larvæ, the latter aperture is absent. In others it is only developed towards the end of this stage of life, when an excrement—or *meconium* as we may perhaps call it—is for the first time expelled. But though such an intestine might seem to resemble that of the anenterous Infusory, or the hydriform Polyp, we must recollect that it differs from these in the important fact of its not being used for the double purpose of ingestion and egestion. The complications of the above simple canal relate chiefly to its subdivision, and to the addition of blind tubes. A gastric dilatation is the first to appear; its extremities then become constricted, and its calibre enlarged. An œsophagus, a crop or ingluvies, a small and a large intestine, may also be added. Sometimes the supposed stomach is transversely divided into two cavities, and complicated by short cæca. In other instances, longer tubes open into the same part of the canal. While in others, they open into the intestine below this point; and are hence presumed to be biliary.

In the *perfect Insect* the varieties of form are still more numerous and perplexing. Besides the complicated prehensile and dental apparatus, there is often an œsophagus, a crop, a muscular gizzard, a stomach, a small intestine, a large intestine, and a narrower rectum. But development is manifested, not only by differences in the diameter and structure of different lengths of the tube itself, but also by its complication, through the addition of supplementary organs of a more or less tubular form.

The *ingluvies or crop* is present in many but not all of the suctorial genera. It is sometimes distinctly glandular. And even where, as in the Bee, this character is less prominent, it is still probably a secreting organ. But its uses seem to be mainly those of accumulation.

The *gizzard* is generally added to the former organ. It is characterized by distinct muscularity, and a more or less hard or horny epithelium, which is often developed into plates, protuberances, hairs, or teeth. Sometimes it is only rudimentary:—a toothed œsophagus subserving its functions in some insects; while in others, it is reduced to a mere thickening of the muscular wall of this part of the canal.

The *stomach* is also of various form and size. In some insects it is simple; in others it is more or less plicated or cellulated, or its cells are even prolonged into short cæca.

The peculiarities of the remaining subdivisions of the canal are chiefly those of their length and width, and in the degrees of constriction by which they are separated from each other. As yet, however, it has been found impossible to make out any intimate connection between these differences in the anatomy of the tube and the habits of the animal possessing it. Indeed, the general relations of this kind seen in other orders often seem to be interrupted or even reversed in the insects.

The numerous tubes which open into the intestinal canal present still more diversity. They are often named salivary, biliary, or urinary organs. Thus those tubes which open into the earlier part of the intestinal cavity are called salivary; those which empty themselves into the commencement of the small intestine are regarded as biliary; and, finally, those which open into the canal at or near its termination, are considered urinary. It is only the first of these that, after many gradations, fairly attain the glandular development which a conglomerate condition implies. The second vary chiefly in number, and in the frequency of their anastomosis. The third are rarely vesicular in shape.

The digestive canal of the *Arachnida* offers, on the whole, more uniformity. The chief divisions of this order are the parasitic, the spiders, and the scorpions. All are "carnivorous:"—a term which here, as often elsewhere, is only approximatively correct; since most of them do not devour the flesh, but rather suck the juices, of their casual or more permanent victims.

The simple digestive tube of the *Acari* or Mites is prolonged in a straight line from mouth to anus. It is sometimes complicated by gastric cæca or dilatations.

In the *Aranei*, or spiders proper, a slender œsophagus passes back from the mouth to a "stomach." This is sometimes a mere dilatation; sometimes is indicated by four sacculi, that radiate from a narrow tube; and sometimes presents a cavity, having blind prolongations that extend into the bases of each of the maxillary palpi and thoracic legs. All these parts occupy the anterior or cephalo-thoracic division of the body. The remainder of the canal, entering the abdominal segment, dilates, after a single convolution, into a large and sometimes globular intestine, to reach the anus by a short portion, of narrower diameter, called a rectum. The long tubes met with in the Insects recur in this order. One set, of varying size, open in the neighbourhood of the complicated apparatus of prehension; these, from their position, are supposed to be salivary. And occasionally a special poison gland appears to empty itself in this neighbourhood. A middle set, called hepatic, often forms two pairs of tubes, with orifices much posterior to the gastric sacculi; in other cases they are very numerous, and are concealed by a granular mass, which occupies the same situation. The posterior set are one or two pairs of long cæca, which join the intestinal cavity close to its termination, and are hence compared to urinary organs.

The *Scorpions* have a tolerably straight, narrow, and simple tube, complicated by several pairs of straight sacs, which come off at right angles to its anterior part, and are probably gastric crops. Below these, two bifurcating tubes, of great length and small diameter, open into a constriction of the canal. They are regarded as hepatic.

In the order of *Mollusca*, many of whom inhabit the sea, we may again trace a gradual advance of development in the intestinal canal.

The *Tunicata* is its lowest subdivision. Here a simple canal begins by a wide œsophagus, that leads from the bottom of the branchial sac to a stomach or dilatation. This is surrounded by a number of hepatic follicles, that open into its intestinal end; and it leads to a wide recurved intestine, which ends by an aperture on the upper and outer surface of the animal. Sometimes the liver varies from this description in the fact that its follicles are aggregated.

The *Brachiopoda* possess a digestive apparatus of nearly equal simplicity with the preceding. Dental structures are wanting; and the liver is still follicular.

The *Lamellibranchiata* exhibit a somewhat similar condition. Their gastric cavity is sometimes preceded by a short œsophagus. From hence a comparatively simple intestine continues, with a few convolutions, through a mass of liver, to terminate, by a long straight portion, in the anus. The latter segment, or rectum, lies along the hinge of their shell, and often perforates the heart in its course. Although the liver is large and aggregate, it opens by several ducts into the gastric dilatation.*

The *Gasteropoda* have a head, jaws, and salivary follicles. Their longer œsophagus sometimes dilates into an ingluvies or crop. Their stomach often possesses a thickened lining, and a masticatory apparatus of teeth or plates, which make it a kind of gizzard. Sometimes it is divided into two or more compartments. The large liver opens into the pyloric extremity of the stomach, or the commencement of the intestine, by one or more ducts; or, rarely, it empties itself into the œsophagus. One or two large glandular cæca also open into the beginning of the intestine, and are regarded as a rudimentary pancreas. The remainder of the tube is simple, and ends anteriorly in the body, in accordance with the general structure of the animal. In the numerous herbivorous species, the intestine is longer and more tortuous; while the crop, the gizzard, and the masticatory apparatus all reach a high development.

The intestinal canal of the *Pteropoda* is very similar. It possesses jaws and salivary glands, together with an œsophagus, a crop, a gizzard, a short and simple intestine, and a conglomerate liver that often opens by a single duct.

The *Cephalopoda* exhibit a marked advance of development. Their mandibles form a powerful organ of mastication; and, in many species, salivary glands co-exist. The mouth leads to a long and dilatable œsophagus, which descending, sometimes expands into a crop before it finally reaches the gizzard or muscular stomach. This organ is of tolerably uniform appearance. Its shape is round, or somewhat elongated; it has a thick and whitish epithelial lining, and its muscular layer consists of two sets of fibres, each of which radiates from a central tendon on one side of the organ. The cardiac and pyloric orifices are situated at its upper part. The intestine coming from the latter soon communicates with another cavity, which is sometimes regarded as a stomach. This is, in the lower Cephalopods, nearly spherical. But in many of the higher or Dibranchiate division, it is of less simple form, being triangular, elongated, or folded spirally like a snail shell. Its mucous membrane is rugous and follicular; and the large liver, which is still supplied by arterial blood, opens into it by a single duct. The intestine continues hence as an uniform tube, which, after one or two slight curves, bends upwards to open at the base of the funnel. In some species we also find cæcal appendages, the ducts of which join those of the liver before they enter the

* In some species a curious style or hard conical process occupies a tube of similar shape, that communicates with the gastric dilatation. The use of this implement is unknown; but it has been suggested to effect a triturative process:—a supposition which, if true, would render the cavity containing it the analogue of a gizzard.

intestinal cavity. These have been supposed to constitute a rudimentary pancreas.*

The alimentary canal of *Fishes* is simple, wide, and short, compared with that of other Vertebrata. Its chief subdivisions are an œsophagus, a stomach, and an intestine.

The *œsophagus* is large, dilatable, and muscular. Its mucous membrane is generally simple, sometimes involuted or glandular; and offers a remarkable contrast to the redder and more vascular membrane of the stomach at the point of their junction. As the diameter of the tube rarely undergoes any great and sudden increase in this situation the above contrast of structure is often the only distinction between the two cavities.

The *stomach* varies greatly in size and shape. Usually, however, it forms a curved tube like a siphon. The obliteration of the concave side of this tube converts it, by many gradations in different genera, into the shape of a two-necked flask, or of a blind tube with a double orifice at one end. In other instances it is dilated, or almost globular. Where tubular, it generally tapers away towards the pylorus. And this end of the stomach, which is usually more muscular than the cardiac, sometimes approaches the structure of a gizzard, having constricted extremities, a thick muscular coat, and a scaly epithelium on its mucous membrane. The valve itself is almost always present, as a circular ridge of muscular fibre, covered by a fold of mucous membrane.

The *intestine* of the fish is short and wide: and generally consists of two portions, which are separated from each other by a slight constriction into a small and large intestine. The first receives the bile-duct, and the follicles which form the rudimentary pancreas. The latter also occasionally receives a cæcal tube. The intestine has the usual three coats—serous, muscular, and mucous. The serous membrane is often pigmentary, and its cavity communicates by apertures with the exterior. It rarely forms a continuous mesentery: — the attachment of the intestine being generally ligamentous or filamentous, or even, as in one instance †, by means of a mass of areolar tissue that involves the whole tube. The muscular coat is of unstriped fibres ‡, which form two layers, the circular generally external.§ The mucous membrane is variously folded: it sometimes contains ductless glands: rarely it is ciliated.|| The chief deviations from these the ordinary characters of the intestine are, either an increase of length, which is sometimes accompanied by a diminution in width; or an equally real increase of active surface, which is due to the development of folds, such as the spiral valve of the Shark.

The *appendices pyloricæ*, or pancreatic follicles, are absent in many fishes. They vary in number from one to two hundred. In structure they range from simple, short canals, to elaborate branches, which are united by areolar tissue and vessels, and are enclosed in a muscular tunic.

The alimentary canal of *Reptiles* preserves much of the simplicity, width, and shortness, seen in that of Fishes. But it offers important differences in many respects. The thick, semi-transparent, gelatinous-looking intestinal parietes generally possessed by the Fish, are strongly contrasted with the thinner and more condensed and opaque tube present in the Reptile. Such a comparison seems to indicate a great advance in the development of the Reptilian digestive canal. This advance, though no doubt correlative with that of the tissues generally, probably depends chiefly on the increased efficiency of the respiratory function.

The *œsophagus* varies greatly in size and appearance. It is usually large and dilatable. In the Ophidians this width and laxity are so greatly increased, that it forms a tube which can be distended to almost any extent; and the parietes of which are so thin, that they may be regarded as supplanted by the muscular parietes of the belly itself.

The *stomach* rarely possesses any well-marked cardiac constriction. Hence the characters of its mucous membrane are the chief means by which it can be distinguished from the œsophagus. Its form, in the Chelonian and Batrachian divisions, somewhat resembles that seen in many fishes. Beginning by a dilated cardiac pouch, it tapers away towards the pylorus, taking a curve like a siphon. In the Crocodiles, the stomach may be regarded as consisting of two portions. Of these, the first is a gizzard: which resembles the form and appearance of that of the Cuttle-fish; and consists, like it, of a plane of muscular fibres, that radiate from a central tendon on each side of the organ. The second is a small pyloric pouch or diverticulum, which passes out of the gizzard at its upper part, close to where it receives the dilated œsophagus. In many Serpents the pyloric extremity is so narrow and muscular, that the organ has been distinguished into two parts:—an upper, or cardiac, which is thin and saccular; and a lower, or pyloric, which is narrow, strong, and tubular. The pyloric valve varies in development. But even where best marked, it never approaches the distinctness seen in man and the higher Mammalia. It consists, as usual, of a projection, which is formed by the circular muscular fibres, and is covered by a fold of mucous membrane.

The *intestine* is short, and rather wide. It is usually divided into small and large by a circular constriction or valve.

* Many anatomists, however, consider the office of this gland to be fulfilled by the cavity previously mentioned. But strong arguments against this view might be derived from the development of glands in general, and of the pancreas in particular; both in the phases of individual life, and in the advance of the animal series. In addition to this, the gastric character of this cavity, and the unfitness of a gizzard for solvent or digestive functions, further justify us in preferring the above interpretation.

† The *Tetrodon mola*.

‡ In the Tench (*Cyprinus tinca*), they are striped.

§ Reversing their ordinary arrangement in the Mammalia.

|| As in the *Branchiostoma*.

In the *Batrachian* division, however, the separation into these two segments is sometimes absent. While sometimes, as in the Toad and Frog, there is a distinct large intestine, into which the smaller portion opens laterally, so as to form a cæcum. In the former of these two genera there is no valve.

In the *Ophidian* the two portions are generally distinct and short. But their relative extent varies considerably: the small intestine being sometimes lengthened, and often presenting a very peculiar appearance in the shortness of its mesentery and the closeness of its folds. The indistinct ilio-cæcal valve is chiefly marked by a change in the diameter of the tube. The large intestine is often subdivided into distinct portions by one or two transverse valves.

In the *Chelonia* the intestine is longer and much more muscular. There is generally an ilio-cæcal valve, and often a well-marked cæcum. The valve is also present in most of the *Sauria*. But in the Crocodile the cæcum is absent.

Birds.—In this class, the *stomach* is generally complex; being separated into three distinct cavities, which differ greatly in their form, structure, and office.

The *œsophagus*, which leads to the first of those cavities, has a length corresponding to that of the neck which it occupies. Its width and dilatability mainly depend on the nature and form of the food. Thus, in some of the birds of prey, or those which swallow large fish entire, it is very lax and dilatable. And in this respect, as well as in the direct continuity of its cavity with that of the stomach, it offers a great similarity to the gullet of the Ophidian reptiles and many fishes. Its mucous membrane is follicular, and folded longitudinally.

The *ingluvies*, or *crop*, is a dilatation of the œsophagus, somewhere about the middle of its length. In some of the smaller Raptores it is but small; in the larger and more voracious it is a considerable enlargement, that affects one side of the tube more than the other; in the Gallinaceans it is a distinct sac, appended to the canal by a narrower neck; and, finally, in the Pigeons, it attains its maximum size, and becomes double. Its muscular and mucous membrane are similar to those of the œsophagus. The food which it contains undergoes a kind of insalivation and maceration. And the highly-developed form of crop, which is seen in the Pigeon, pours out a milky fluid during that period of the year in which this bird feeds its young by regurgitation. At this time its mucous membrane also acquires a thicker and more glandular character.

The *proper stomach*, or *proventriculus*, communicates with the inferior part of the œsophagus, and corresponds, both in structure and function, with the true stomach of the *Mammalia*. The glandular tubes which open on its free surface secrete a fluid that possesses all the properties of gastric juice. In the degree of complication these glands differ considerably; varying from simple tubes in the carnivorous birds, to tubes that open between prominences and prolongations, and finally form primary and secondary branches. The shape and size of this organ are subject to great variety in different genera. In those that swallow a large prey, it is wide and straight, like the stomach of the Serpent. In others, it approaches the spherical form, or passes towards the right side to join the gizzard. The comparative size of these two organs also varies considerably.

The *gizzard* is a flattened ovoid of highly muscular texture. It is lined by a dense horny cuticle, and contains sand, gravel, or other hard inorganized matters, which are the passive agents in the trituration of the food. Its size varies greatly. Its apertures both occupy the upper part of the organ, so that its cavity terminates below in a blind extremity. Its walls contain a variable amount of muscle, the arrangement of which is usually that of the radiation of fibres from a central tendon, such as was previously noticed in speaking of the Cephalopoda. Its epithelium is hardest in the granivorous birds. And even in the same individual, it offers an increased density at the precise situations of most pressure. In like manner, Hunter noticed that a thickening, both of cuticle and muscle, was produced by feeding a Sea-gull upon grain.

The pyloric valve is, as a rule, well marked. In some species there is a small supplementary cavity, which immediately precedes it, and receives the orifice of the gizzard.

The *intestine* has a length about midway between that of the Reptilian and Mammalian bowel. But although longer than in either of the preceding classes, it retains considerable simplicity of form. It presents, however, much variety, both in its length and in the number and appearance of its convolutions;—differences which, as usual, are related (though not very closely) to the food and habits of the animal. The duodenum which immediately follows the pylorus has the form of a long loop or fold, the concavity of which includes the pancreas. The small intestine, more or less folded, terminates in a large intestine, the commencement of which receives two cæcal tubes, one on each side. These cæca offer remarkable differences in length:—varying from papilliform offsets, as in the Solan-goose, to processes three feet long, as in the Grouse. Sometimes only one is present. The short and straight large intestine is continued from the termination of the small intestine, without any distinct valve, to end in a cloaca common to the digestive, urinary, and generative organs. Connected with the small intestine is an appendage, supposed to be a relic of the duct of communication between the yolk bag and intestine of the chick. It is devoid of a muscular tunic, and in some birds equals or exceeds the size of the cæca themselves.

Mammalia.—The form, length, and arrangement of the alimentary canal vary so much in the different orders of Mammalia, that it will be necessary briefly to state its peculiarities in each.

In the *Carnivora* the shape of the stomach approaches that of the human organ: it has a cardiac pouch, and a greater and lesser curvature. The intestine is short, its length being to that of the body as* 5 to 1 in cats and dogs, and 8 or 9 to 1 in the hyæna and bear, but reaching 15 to 1 in the *Phoca vitalina*, one of the amphibious seals. The mucous membrane is destitute of folds. The convolutions of the small intestine are few and simple. The cæcum is short, and scarcely wider than the rest of the large intestine.† And the latter segment of the canal is short, wide, and cylindrical.

The *Insectivora* have a very similar intestinal tube. The simple and elongated stomach is transverse to the axis of the body. In some genera, its spherical cardiac pouch is enlarged, while its lesser curvature becomes shortened. The intestine is short—from three to six times the length of the body; it has no cæcum, and a nearly uniform diameter. Its mucous membrane exhibits zig-zag folds, which run longitudinally throughout its whole length.

In the *Cheiroptera* three chief varieties of stomach have been distinguished by Cuvier. The first approaches that seen in the preceding order, and belongs to those members of this group which feed upon insects. Here the nearly spherical organ has a cardia and pylorus, which are situated close to each other. The second form is seen in those which subsist by sucking the blood of animals: it differs from the preceding in being longer, and more conical from cardia to pylorus. The third, which obtains in the frugivorous division, is very different from both the preceding.

Thus, in the *Pteropus* the stomach is a long tube, placed transversely to the axis of the body. One-third of its length is formed by the cardiac pouch, which lies to the left of the œsophageal aperture, and is divided into two by a slight constriction, while its terminal or pyloric third is bent back so as to be parallel and near to the middle portion. The mucous membrane of this stomach is folded longitudinally; the left subdivision of the cardia is smooth, and the lower part of the œsophagus — which is somewhat dilated — differs from the upper.

The pylorus is well marked in all the Cheiroptera, and the intestine, which is much narrower than the stomach, and is devoid of cæcum, is of nearly uniform diameter. It often presents concentric windings or coils. Its length varies greatly;—thus, in the frugivorous Pteropus it is six or seven times, in the insectivorous Bat only twice, the length of the body.

Edentata.—The stomach of this order differs greatly in different genera. Most of them possess a simple organ; the cardiac pouch of which is large and globular, while the pyloric extremity is conical, and is sometimes almost absorbed into the spherical cavity. A single genus, the *Manis*, adds a further distinction to these two parts in the shape of an internal fold of mucous membrane; and one of its species exhibits a long blind sac, springing from the right of the pyloric aperture. In the *Tardigrade* genera the stomach assumes much of the complexity seen in the Ruminantia. For it has two cavities, a cardiac and a pyloric, which, if regarded from the exterior, look like mere exaggerations of the distinction mentioned above, but, when examined internally, are seen to be divided by prominent folds, and by differences in the character of their mucous membrane. Thus the cardiac pouch has a dry epidermoid lining, and is subdivided by a fold into two parts, and prolonged into a short blind tube, while the pyloric sac has a soft and delicate mucous membrane, and more muscular parietes. And its interior is also subdivided, by a fold of membrane, into a terminal part, which is analogous to the fourth stomach of the Ruminants, and an intermediate cavity, which resembles the third stomach of the same order in its possessing dentate processes, and a direct communication with the œsophagus. The latter tube also exhibits a *cul-de-sac*, which is sometimes further divided by folds.

The form and length of the remainder of the canal is subject to great variety. Its mesentery is very long. In many genera there is no distinction of the intestine into large and small. In some there is no trace of a cæcum. In others there are two of these tubes, which occupy the confines of the large and small intestines, and open by what are sometimes extremely minute apertures.*

The *Ruminantia* are remarkable for the complete subdivision of their stomach into four distinct cavities. The first of these, the *rumen*, or *paunch*, is generally of very great size. It is situated to the left of the œsophagus, from which it receives the food when first swallowed: it has a villous texture, but its minute conical processes are covered by a dense white pavement epithelium. The second cavity, the *honeycomb* or *reticulum*, is so called from the appearance of its mucous membrane, which, in all other respects, has the same structure as that of the preceding cavity. The third portion, the *maniplies* or *psalterium*, is named from the many longitudinal plies or folds which occupy its interior. In the Camel, the circumference of the cells or excavations of its reticulum and paunch have been long recognized as containing muscular fasciculi, the contraction of which enables these cavities to retain water free from admixture with the general contents of the stomach. And

* We owe these measurements to Meckel.

† In the dog it is convoluted.

* In such a case they can hardly be supposed to receive fæcal matter. But in the *Dasypus mustelinus*, the ileum ends by a slit between the larger apertures of two such tubes; and hence appears to admit of being closed by the lateral pressure of their contents. (See Prof. Owen's Catalogue of the Hunterian Museum, vol. i. p. 219. 729 A.)

eight or nine years ago, the author discovered that all these projections from the surface of the ordinary Ruminant stomach,—viz. the villi, honeycombs, and plies—are constructed chiefly of unstriped muscular tissue, lined by scaly epithelium. The uses of such a structure are too obvious to need any comment. The fourth cavity or *abomasum*, is the true stomach: it secretes the gastric juice, and possesses the ordinary tubular structure. As regards the uses of these cavities, the bolus is probably moulded for rumination in the honeycomb, and is thence regurgitated into the gullet; while a muscular fold forms a direct pathway for the ruminated food to pass at once from the œsophagus to the maniplies.

Pachydermata.—The Elephant has a stomach which is elongated, and subdivided by very numerous folds. In other respects it is simple. That of the Rhinoceros is similar; but the cardiac pouch is devoid of folds. The shorter stomach of the Pig is divided internally by two folds of mucous membrane into three portions:—a cardiac pouch, a pyloric extremity, and an intermediate portion, which receives the œsophagus. The lesser curvature, and the back of the cardiac pouch, are both occupied by a white and dense epithelium, which is similar to that of the œsophagus, and forms a broad quadrilateral band along this aspect of the interior. In the Pecari there are external indications of the same subdivisions: but the white epithelium extends over a wider surface; so that it is only the pyloric third, and the lower parts of the middle and cardiac pouches, which exhibit the proper gastric or tubular structure. In the Hippopotamus, the stomach is long and tubular, and is complicated by the addition of two pouches, which have a size almost equal to its own, and communicate with its cavity by corresponding orifices on the right of the œsophagus and at the back of the cardia. The internal surface of the organ is so folded as to allow the alimentary bolus to enter either of these two cavities.*

The stomach of the *Solipeda* has a rounded shape, and a cardia and pylorus which are close to each other. The cardiac half of the organ is lined by a white epidermis, which terminates by an abrupt dentated margin.

In all these three orders — Ruminants, Pachyderms, and Solipeds—the *intestine* is characterized by great length, width, and convolution, and by the possession of a capacious cæcum. Thus, in the Ruminant sheep, the intestine is thirty times the length of the body. And although in the Soliped horse this proportion sinks to fifteen or twenty, still the sacculation of the cæcum and colon which obtains in this and the Pachydermatous order perhaps compensates such a diminution in length. The ilio-cæcal valve is represented by a narrow passage, the mucous membrane of which forms six or eight thick longitudinal folds. The cæcum, smallest in the Pachyderm, attains its maximum size in the Soliped; being, in the Horse, two feet long, and thrice as capacious as the stomach. In one Pachyderm—the Cape Hyrax—two additional cæcal tubes open into the large intestine by wide apertures.

In the *Rodentia* the stomach is separated by an external constriction into two portions: —a cardiac, clothed with a thick epidermis, and a pyloric, occupied by a mucous membrane which has the ordinary tubular structure. The size of the former pouch varies in different genera; the latter sometimes presents an imperfect subdivision. The whole organ occasionally approaches a conical or spherical shape. In the Beaver and Muscardin, the stomach is complicated by the addition of glandular crypts and cæca, the import of which is unknown. The intestine of the Rodent is very long and convoluted, and the small and large intestine are of nearly equal diameter; but the latter is deeply sacculated. The cæcum is usually very large, and is sometimes subdivided by spiral or circular folds. But in the omnivorous Rat it is small; and in the Dormouse it is altogether absent.

Marsupialia.—In a large proportion of this order, the stomach has a considerable resemblance to that of the human subject. Such an organ is found in both carnivorous and herbivorous Marsupialia: and indeed, it is difficult to point out any differences in its size or shape which are distinctly referrible to the habits of its possessors. In some, however, a stomach of very similar outside shape exhibits a lesser curvature, which is occupied by a gastric gland like that of the Beaver, composed of numerous irregular crypts. In the Kangaroo (*Macropus*) both the shape and the structure of the organ differ widely from the preceding. The stomach is of a length which equals that of the whole body; the cardiac pouch is subdivided into two cæca; and the middle part of the organ is sacculated by three bands of longitudinal muscular fibres, so as closely to resemble the ordinary arrangement of the colon,—except that the interspace between the upper two, or that third of the surface which occupies the lesser curvature, is not sacculated. The gastric gland is broken up into numerous follicles, which are placed in three rows parallel to the longitudinal muscular bands. The mucous membrane of the œsophagus is continued right and left of the cardiac orifice for a considerable distance; somewhat as in the stomach of the Pig. The remainder of the mucous membrane is of the ordinary soft character.

The intestine of the Marsupial is also subject to great differences. The carnivorous members of the class are devoid of a cæcum,

* The above is a description of the organ in the fœtal Hippopotamus, to which alone our present information refers. Cuvier suggests this to have been an incomplete development of a compound organ, akin to that of a ruminant: the stomach being the abomasum, and the diverticula representing the paunch and honeycomb. But the tough and wrinkled character of the mucous membrane which lined the supposed abomasum in the greater part of its extent seems to negative this view.

The insectivorous Marsupials have a longer intestinal canal, which is separated into large and small intestine, and exhibits a cæcum of moderate size. Those that live upon fruits have bowels which are still longer, and a large cæcum of twice the length of the whole body. Finally, the true vegetivorous genera have a cæcum which is thrice as long as the body. In those which are possessed of a sacculated stomach, the cæcum is, however, much shorter. One genus, the Wombat, has a vermiform appendix. The length of the whole intestine varies from two to ten times the length of the animal.

In the *Monotremata* the alimentary canal is chiefly remarkable from its terminating in a cloaca common to it and the urinary and generative organs. A small cæcum separates the long and narrow bowel into two parts. The diameter of the small intestine gradually diminishes to the cæcum, while that of the large intestine gradually increases to the rectum.

The *Cetacea* offer two chief varieties of stomach, which are connected with differences in their food, though scarcely explained by them. Those which live on vegetable food exhibit a simpler form of organ. Thus, in the Dugong, the stomach is long and transverse; and is divided by a deep constriction into a globular cardiac, and a conical pyloric, portion. Two large cæca open into it near this constriction; and a special glandular apparatus occupies the upper part of the cardiac pouch. In the carnivorous Cetaceans, the stomach is subdivided into three, five, seven, or more cavities. In some genera, however, there are only four. Of these the first has an epidermoid lining, while the three last have a soft mucous membrane. The biliary duct often opens into a dilated cavity, the import of which is unknown. The intestine is longer in the herbivorous division. Here there is also a cæcum; which is sometimes large and glandular, but sometimes small, short, and even bifid. In the zoophagous Cetaceans there is rarely either cæcum or valve:—so that the intestine, which decreases slightly in size from the pylorus to the anus, offers no separation into large and small. But in the genus *Balæna* there is a small cæcum, like that of the Cat.

The *Quadrumana* possess a stomach the form of which approaches that of the human organ. In some cases, however, it is more elongated; while in others it assumes a globular shape, with a cardia and pylorus in close proximity. The latter deviation is generally found in conjunction with carnivorous or insectivorous habits. It is usually separated into two portions, a cardiac and a pyloric; and sometimes the latter, which is more globular than usual, is distinguished by an internal fold from a short tubular part, which terminates in the pyloric valve and the duodenum. Rudimentary pyloric cæca have been remarked by Cuvier * in one instance. The *Semnopithecus* presents a form of stomach which recalls that of the Kangaroo. For the cardiac cavity, smooth and almost bifid at its commencement, is soon sacculated by a superior and inferior band of longitudinal fibres which come from the œsophagus; and from thence the stomach continues to the right side, as a sacculated tube, which is bent upon itself, and closely resembles a large intestine. But before reaching the pylorus, these sacculi diminish and disappear.

The length of the intestinal canal in the different genera of this order varies to an extent which is curiously contrasted with the general similarity of their food. Its proportion to the length of the body is in some as 8 to 1; in others as 3 to 1 only. The division into two portions, and the general arrangement of both small and large intestine, is very similar to that seen in man. In all the genera a cæcum exists, but with great variety as to length:—an increased development of this portion of intestine, as well as of the cardiac extremity of the stomach, being sometimes connected with a diminution in the length of the whole canal. The Apes and Gibbons possess a vermiform appendix; but in the latter it is of very small size. The mucous membrane has villi, but no valvulæ conniventes.

General remarks.—Although physiology at present scarcely pretends to interpret this various and complex development of the alimentary canal, still some attempt at its explanation is indispensable. For without any clue to their import, details like the preceding could hardly be recollected, far less made use of; and would scarcely deserve to be stored up in the archives of science, much more brought forward in an essay like this. Nor, in attempting their explanation, can one be rightly charged with breaking those rules which our great countryman has laid down for the pursuit of natural knowledge. All that is necessary to such a superstructure of theory is, that, however slight and temporary, it should at least be founded on the known facts; that it should indicate something like the degree of probability assignable to its several parts; and, finally, that it should be at once yielded up, as soon as a stricter logic, or larger and more numerous facts, offer us a better explanation.

The absence of all digestive cavity is the first peculiarity which demands our notice. The few genera in whom this rare condition has been found all offer the greatest simplicity of structure; and further agree in the fact that they are parasitic:—*i.e.* that they derive their nutriment from the juices of another animal, to whose body they are attached. Hence we need not scruple to assign this apparent deficiency of the digestive organ, partly to the previous elaboration of a highly nutritious animal food, partly to the simplicity of the various tissues which are destined to be nourished by it. But can we therefore say, that the function of digestion is absent, or — what would be nearly equivalent to such an assertion — that it is reduced to a mere physical absorption? Probably not. For, as regards the general development of the animal series, comparative

* Leçons d'Anat. Comp. vol. iv. p. 28.

anatomy conclusively shows that the fusion of certain structures by no means implies the absence of their several functions; while a history of the development of each individual would equally establish that, though the embryo at a certain stage of life is quite devoid of a digestive cavity, it is nevertheless nourished by materials which have been previously set apart from the substance of the parent. And just as it must doubtless effect some change in these materials, in order to assimilate them to its own various textures, so it is evident that such a change, however slight, probably represents what is as much a digestive as an absorptive act:—a digestion in which the absence of many of the ordinary agents is sufficiently accounted for by the minimum of waste which this food supplies, and the minimum of change which it has to undergo. Now some of these parasitic genera are also connected by the circumstance, that the anenterous condition probably forms but a stage of their development;—so that the process of time, or their transplantation to a more congenial dwelling, would often convert them into animals possessing an alimentary canal. Of such creatures we might therefore vaguely say, that they retain the low digestive development of an early ovum; or, in other words, that they are themselves the partially developed embryos of a very simple organization. That, with such a simple structure, they should effect such a complex function, is surely not one whit more extraordinary than what appears to be the case in the action of every ordinary cell; which is what it is—liver, kidney, or the like—by virtue of powers that its mere structure will not explain—powers that enable it to attract and retain certain materials, to relinquish or dismiss others, or even to effect a definite metamorphosis in its own chemical ingredients.

The simplest form of the digestive organ may be seen in the hydriform Polyp, as a cavity of the body, in which the food undergoes a kind* of solution. The agent of this process is doubtless a fluid which exsudes from the membranous walls of the cavity. But as these are also the parietes of the body, it is to the latter that we must probably refer the origin of the solvent. That harmless inversion of the whole animal, which Trembley was able to effect, strengthens such a conjecture. Nor is it impossible, that the poison of the tentacles is itself but a more concentrated form of the gastric fluid. In any case, one cannot avoid suspecting that, in this animal, the alimentary solvent has some very simple chemical relation to the organism generally. The more so that, although it acts upon the swallowed prey with the greatest energy and rapidity, the tentacles of the animal itself, which are often closely entwined around the hapless victim, are quite unaffected by even a prolonged stay in the stomach. And the same impunity extends to another animal of its own species which may have been swallowed while tenaciously clinging round the prize * that both are disputing.

It is usual to call such a simple digestive cavity a "stomach." But though the etymology of the term quite allows of its being thus applied, still the definite character of this organ in the higher animals seems to suggest that we should either restrict its application, or recollect the doubtful meaning which it acquires by such an extended use. Whenever an organ of this kind appears to effect the solution of substances which pertain to the albuminous group†, it is entitled to rank as a true stomach. But in proportion as this fact is uncertain or improbable, the name becomes a vague designation, which ought never to be made use of without recollecting what it really means—a mere receptacle of food. In the instances before us, such a receptacle probably represents, not only the stomach of the higher animal, but a fusion of this with the succeeding ‡ portions of the tube, and with all the accessory organs of digestion,—such as the liver, pancreas, &c. And just as such simple cavities import more than a mere gastric function, so conversely we might find others bearing the same name, which complicate a fully developed alimentary canal, and thus imply less. These, though called stomachs, are probably mere crops.

A *complex digestive organ* might at first sight seem to be the natural antithesis of the preceding. But though complexity forms a useful subjective contrast, without which we could indeed hardly conceive of simplicity—still, as already hinted, instead of a progressive evolution, corresponding to a gradual and successive advance of development, the alimentary canal rather offers a variety of deviations. And most of these deviations appear to result from causes, the number and intricacy of which is such as to defy all analysis. We shall therefore only enumerate those, the influence of which seems to be most direct and important.

1. It is scarcely necessary for us to dwell upon that advance of development, and gradual increase of complexity, which the reader must have observed in the preceding sketch. He has seen how, in progressing from the lowest Infusory to the highest Mammal, a simple excavation first became a membranous canal; how it then acquired an additional orifice; an organ of mastication; a salivary apparatus; a stomachal dilatation; a subdivi-

* For the sense in which we are to understand the word solution as applied to this process, see the remarks upon the action of the gastric juice at p. 337.

* It is interesting to notice that differences of development, such as are obviously almost tantamount to diversity of species, appear to remove all barrier to this solvent action. Thus the Polypiform Medusa devours and digests its Infusory-like younger brethren.

† See p. 335.

‡ The term "chylific stomach," sometimes made use of by comparative anatomists, seems especially to demand such a caution. For we need scarcely point out that, in the higher animals, at any rate, this organ does not "make chyle."

sion of intestine; a liver; a pancreas; and, finally, a compound character of mucous membrane, by virtue of which the whole tube might be compared to one vast expanse or aggregation of glands. Some of these particulars will again force themselves upon our attention. Hence we may here limit ourselves to the remark, that the main elements of this advance consist in the evolution or separation of accessories, and the increase and subdivision of surface:—and that both of these conditions imply a division of labour which, here as elsewhere, enhances both the quantity and quality of its product.

2. Respecting the homologies of the intestinal canal, scarcely anything can be said. As might be expected, form seems always subordinate to purpose:—in other words, neither general nor individual development offers us any permanent or temporary organs of digestion, from which we can deduce a shape that can be considered as a common pattern or archetype.* In rare instances,—as in the Earth-worm and Arachnidan,—the form of the internal canal approaches that of the body and limbs respectively. But even this peculiarity of form is probably teleological.

3. Sufficient allusion has already† been made to vegetative or irrelative repetition, as a possible explanation of the complex canal seen in many of the lower Invertebrata. Some of these ramified canals — such as those of the Acalephæ, and, with less probability, of the Distomæ — may be conjectured to represent a vascular, rather than intestinal, system. But there are others — such as those of the Leech and Spider— which seem to be true processes of the digestive canal, used as reservoirs of food.

4. Some complications seem mainly dependent upon circumstances which may be termed collateral or subordinate to digestion itself. Thus, the crops of many animals, like the cells of the Camel's stomach, are connected with the more or less necessary habit of gorging large quantities of food at distant intervals. While the gizzard, which is possessed by such very different orders as Polyps, Molluscs, Fishes, and Birds, appears to be closely related, not only to the food, but to the mechanical conditions of the animal. This is especially the case with the Bird, whose long neck, and habits of flight, could scarcely be rendered compatible with a heavy masticatory organ occupying the ordinary position.

5. The import of some of those numerous blind tubes or pouches which we have so often noticed as opening into the intestinal canal, has already been suggested in the preceding remarks. They are generally, and no doubt correctly, regarded as earlier developmental forms of the various conglomerate glands which are appended to the canal in higher animals. But as regards the principles of their diagnosis, and the limits of its application, it seems important to remind the reader, that, in the present state of organic chemistry, the situation of their apertures, and the order of their appearance, often constitute our only guides. Thus, for instance, tubes which open into the commencement of the canal, especially in connection with a higher development of the masticatory organs, are probably salivary. In like manner, those which empty themselves in the neighbourhood of the pylorus are supposed to be biliary. And any which, by communicating with the anus and exterior of the body, appear to aim at an immediate and direct extrusion of their contents, naturally remind the physiologist of the highly poisonous characters of the urinary secretion, and so far entitle him to suspect that they serve to expel this important product of animal life. Here, however, chemistry would often assist his decision. The colour of the bile sometimes affords a less certain aid to the diagnosis of this secretion. The order of appearance only helps our conjectures by showing, that, of the two glands which open into the median portion of the digestive tube, the liver is the more constant and important:—and hence, that it is probable a solitary set of tubes are chiefly hepatic. But it is obvious that, in many instances, all these aids to conjecture may leave us in doubt as to the true nature of a set of secerning tubes.

6. In many of the Vertebrata — such as Birds and Edentata—there are cæca to which, as to the smaller vermiform appendix of man, the above explanation cannot apply; since the ordinary accessory glands are also present. And some of the tubes seen in Insects are probably quite as supplementary. The structure of all these tubes seems to indicate that they are true organs of secretion. But whether this is their main function — or if so, what is the nature of their product — is utterly unknown. The supposition of their possessing a special absorptive function only increases this obscurity, by leaving it doubtful whether the lower parts of such tubes reclaim a portion of the secretion poured out by the upper — just as the intestine absorbs the bile after its entry into the duodenum — or whether they absorb materials derived from the general cavity of the intestine. But that increase of surface which facilitates mere absorption is effected by folds and projections so much better than by tubes, that, even supposing this latter reabsorption to obtain, we ought at least to concede some modifying power to the secreting surface. The ordinary situation of their apertures — near the junction of the small and large intestine — scarcely assists our speculations. It may, however, indicate an exposure of their secretions to the long and energetic absorption effected by the large intestine.

* In this respect the intestinal canal may probably be contrasted with both the vascular and nervous systems. At least the author feels sure that the latter of these will ultimately be found reducible to that serial homology of the skeleton which the researches of Professor Owen have done so much to elucidate.

† See p. 295.

7. Finally, we may close these vague conjectures by attempting to include, in one formula, most of the varieties seen in the whole animal kingdom. The complexity of the digestive apparatus varies with that of the digestive function. And this is again the product of two chief elements:—the kind of food used; the nature of the animal to be nourished.

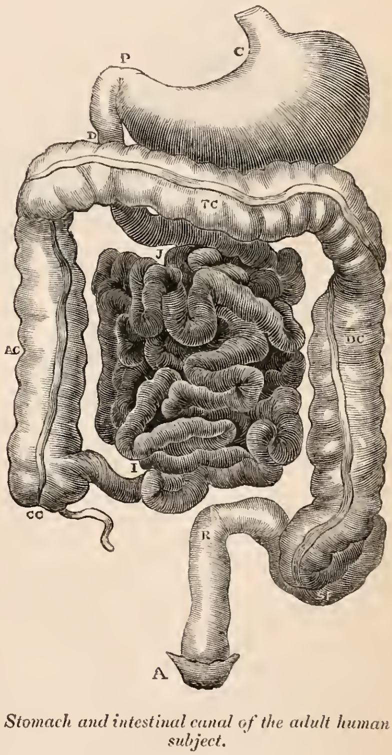
In respect to the food, we might almost form a scale of decreasing simplicity, beginning with the rich chylous fluid that bathes the intestinal parasite, and passing through the various gradations of *liquor sanguinis*, blood, flesh more or less decomposed, vegetable juices, fruits, vegetables, and grains: — gradations which, however increased in number and minuteness, would all find their corresponding representatives in Natural History. And we have already seen that, throughout the Vertebrate series, there is a constant association of a long intestine or a complicated stomach, with a vegetable diet.

As regards the nature of the animal, the Acalephan, Crustacean, Cephalopod, Fish, Bird, Cetacean, all prey upon fish. Yet not only are their organs of digestion most diverse, but they even exhibit a certain correspondence with the general development of each animal. Nor is it difficult to imagine why this is the case. Looking only at the unity of the organism, we might *à priori* expect, that a high development of the whole would imply an equal advance in the complexity of its chief parts. To this we may add, that one organ seems in a certain sense complementary to another,—the necessary, and not merely the formal, result of an increased evolution of its fellow. And, in conclusion, it is not unlikely that the complexity of the digestive organ in the higher animals may be referred to causes even more immediate than either of the preceding: — viz., to the more composite chemistry of their structure, and the more rapid and energetic change of their substance. The structure of every animal is so far self-regulative, as to determine the permanence of its own composition, by a process of which the blood is one main agent, and the tissues generally another. But there is no reason why we should exclude a third — why we may not suppose that the chemical assimilation or likening of the foreign substances taken as food is commenced in the course of the digestive act — why, in short, the absorption of more numerous, abundant, and complex alimentary principles may not necessitate the co-operation of a more highly developed digestive organ.

Human Anatomy.— The alimentary canal of Man is a long membranous tube, which, commencing at the mouth, successively occupies the regions of the neck, chest, belly, and pelvis, to terminate at the lower orifice of the latter cavity in the aperture of the anus.

In this course, the canal first forms at the back of the mouth a dilatation, called the PHARYNX. It next contracts into a straight cylindrical tube, the ŒSOPHAGUS, which is continued through the neck and chest. Immediately after perforating the diaphragm, or septum which divides the thorax from the abdomen, it expands into the STOMACH (C, *fig.* 241.). An external constriction and an internal valve (P, *fig.* 241.) mark the boundary between this organ and the INTESTINE, which forms the remainder of the tube. And, finally, at about five-sixths of its length, the intestine is subdivided into two portions, by an alteration in size and character, which commences at a point corresponding to the presence of a cæcum or blind pouch externally, and of a valve internally. Of these two segments, the upper, longer, and narrower, is called the SMALL INTESTINE (J, I, *fig.* 239.); and the lower or wider, the LARGE INTESTINE (CC, AC, TC, DC, SC, R, *fig.* 239.).

Fig. 239.



Stomach and intestinal canal of the adult human subject.

C P, stomach; C, cardiac; P, pyloric orifice; J I, small intestine; J, jejunum; I, ileum; C C to A, large intestine, viz.:—C C, cæcum; A C, ascending colon; T C, transverse colon; D C, descending colon; S F, sigmoid flexure or sigmoid colon; R, rectum; A, anus.

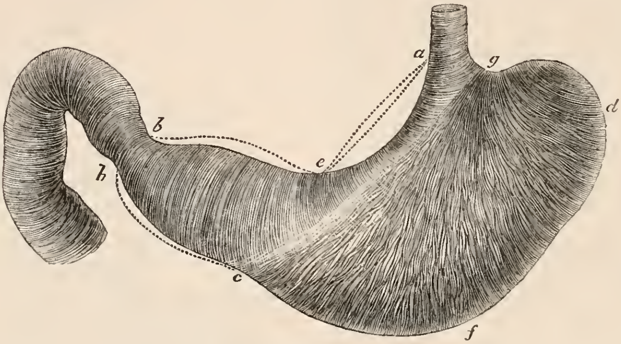
It is the three latter portions of the alimentary canal,—viz., the stomach, small intestine and large intestine,—which form the especial subject of the following article. They all possess the same general structure; being composed of three coats or tunics — an external and serous, a middle and muscular, and an internal and mucous coat. The first of these constitutes their means of attachment to the trunk in which they are enclosed; and it limits, permits, and facilitates those movements, which it is chiefly the office of the second to execute. The third is the most important, since it forms the complex secreting and absorbing surface, upon which the functions of the canal mainly depend. Between these three tunics are interposed two layers of areolar tissue; containing vessels, nerves, and lymphatics for their supply. The various modifications undergone by these constituents of the tube, in the three segments just distinguished as the stomach, small intestine, and large intestine, will form the chief features of the following description.

The STOMACH is the widest and most dilatable part of the alimentary canal.

Its *form* varies greatly in different individuals. Removed from the body, and moderately distended, it generally takes the shape represented in *fig.* 240.*; — a shape which is often compared to that of a bagpipe, and may be best described as a bent cone, the concave aspect of which is joined by a tube at one-fourth of the distance from its base. In it we distinguish an anterior and a posterior surface; a superior and an inferior border; a right and a left extremity; together with the cardiac and pyloric apertures, by which it communicates with the œsophagus and duodenum respectively, and thus becomes continuous with the remaining portions of the digestive canal.

The description of these different parts will vary, according to the full or empty state

Fig. 240.



Stomach and duodenum. The tube has been everted and inflated, and its mucous membrane dissected off, so as to show the subjacent muscular coat.

a g, cardiac orifice; *b h*, pyloric valve; *a e b*, lesser curvature, or upper border; *g d f c h*, greater curvature, or lower border. (The dotted lines joining *a e*, *e b*, and *c h* are intended to illustrate the mode in which extreme distention of the organ affects these curves); *g d*, cardiac pouch; *b h c e*, pyloric pouch. (The surface to the right of the line which would unite *c g* represents the oblique, that to the left of this line the circular, layer of the muscular coat of the stomach.)

of the organ. Thus in the latter condition, the stomach is flattened vertically; so that its anterior and posterior mucous surfaces come into contact, while its upper and lower margins form thin edges, each of which really deserves the title of a "border." But when distended, any transverse section of the organ would be nearly a circle; and hence its borders and its surfaces disappear by merging into each other. Its uppermost part, however, is still distinguished as the *lesser curvature* (*a*, *e*, *b*, *fig.* 242.), and the lower as the *greater curvature* (*g*, *d*, *f*, *c*, *h*). It will be seen that the general concavity of the former curve is especially marked in its first half or two-thirds; at the end of which part (*e*) it usually becomes slightly convex. A very shallow notch (*c*) opposite to this point often divides the greater curvature into two portions; and the two constrictions together define the commencement of the *pyloric pouch* (*b*, *h*, *c*, *e*). The *cardiac pouch*, or *great* or *splenic extremity* (*d*), lies to the left of the *cardia* or the œsophageal opening (*a*), beyond which it projects for about three inches. At this aperture the œsophagus dilates gradually, so as to resemble an inverted funnel. To the right of the œsophagus, the stomach expands slightly, and hence reaches its maximum diameter at about the middle of the organ (*f*). Beyond this point it gradually tapers away to the pylorus (*b*, *h*), where a sudden external constriction marks the site of the valve.

The *dimensions* of the organ are even more variable than its form. The author's measurements are not sufficiently numerous to justify him in offering them as valid averages; but he has generally found that, in a state of moderate distention, its length is about 13 to 15 inches, its diameter at the widest part 5, at the pylorus 2, or through the whole organ 4, inches. Hence its total surface would equal about $1\frac{1}{4}$ square feet; and its capacity about 175 cubic inches, or 5 pints. Its weight may be estimated at about 7 ounces. These estimates are a little larger than those of most other anatomists.

The *attachment* of the stomach is chiefly effected by the continuity of its extremities

* This woodcut is so far inaccurate, that the pyloric constriction is shown more distinctly than it could be actually seen in such a view, in which it would be partially concealed by the backward curve of this part of the stomach.

with the more fixed duodenum and œsophagus. The former tube is connected with the posterior wall of the belly, the latter perforates the crura of the diaphragm a little to the left of the median line, so as to enter the abdomen about one inch in front of the left border of the aorta, by an aperture which is everywhere muscular *, although close to the posterior border of the tendon. The fixation of the stomach is also aided by certain processes of peritoneum. To the left of the œsophagus, the short *phreno-gastric omentum* passes from the diaphragm to the cardiac pouch, which it reaches somewhat posteriorly. Still lower down, the stomach is united to the spleen by the *gastro-splenic omentum*. The lower border of the organ gives off the *great omentum* : this descends for some distance towards the bottom of the belly, and is then reflected upwards to the anterior border of the transverse colon, which it splits to enclose. The upper border of the stomach is attached by means of the *gastro-hepatic* or *small omentum*, which descends from the transverse fissure of the liver. All of these folds are double; though the four layers of the reflected *omentum majus* are often inseparably united to each other. They are more particularly described in the article Peritoneum.

Situation. — The stomach is placed almost transversely in the upper part of the abdominal cavity, in which it passes from the left to the right side, as well as downwards, and slightly forwards. This direction results from its situation relatively to the œsophagus and duodenum : since it is joined by the former at its highest part, and near its left extremity ; while the latter is immediately prolonged from its right or pyloric end. In this course from left to right, the stomach successively occupies the left hypochondriac and the epigastric regions; and, just at its termination, it reaches the right hypochondrium. Its anterior surface is therefore in contact with the diaphragm, where this muscle lines the cartilages of the left false ribs ; and with the anterior wall of the abdomen. Its posterior surface lies upon the pancreas, the aorta, and the crura of the diaphragm, where these parts cover the spine. Its left extremity is in contact, above, with the diaphragm, below, with the spleen ; and, posteriorly, it touches the left suprarenal capsule and kidney. Its upper border is in apposition to the liver : — viz. to its left lobe, to the *lobulus Spigelii*, and to part of the *lobulus quadratus*. Its lower border is parallel, and close to, the transverse colon.

Unusual size or distention chiefly affects the situation of the organ by causing it to extend downwards; so as to overlap or cover the transverse colon, and thus reach the umbilical, the left lumbar, or even the iliac region. Under similar circumstances, its left extremity also passes deeply into the corresponding hypochondrium ; so as to be covered, not only by the cartilages of the ribs, but by these bones themselves. Its extension upwards diminishes the size of the thorax, but is rarely sufficient to be felt as a serious hindrance to the descent of the diaphragm in the ordinary tranquil inspiration of health. Its right extremity may reach the gall-bladder.

It may be useful to trace the effect of its usual progressive distention upon the form, site, and fixation of the stomach. When void of food, and not distended (as it often is) by gases, the flattened stomach hangs almost vertically in the epigastrium. In this state of the organ, the pulpy food that enters it from the œsophagus drops at once into the cardiac pouch, which forms its most depending part. The reception of further quantities effaces its upper and lower borders, and gradually changes them,from almost straight lines, into the curves above mentioned ; at the same time that it separates the previously apposed surfaces, and converts the whole organ into a bent cone, which is convex below and in front. The latter of these two flexures chiefly occupies the pyloric extremity, and is often very sudden. Both result from the increased length of the organ, and the proximity of its comparatively fixed orifices. But both are greatly assisted by the muscular coat : since the distention of the separated stomach tolerably imitates, though it scarcely equals, the curves taken by the organ when moderately expanded *in situ*. The delicate and yielding *omenta* above mentioned allow the stomach to expand between their elastic and extensible laminæ, without undergoing any disturbance of its nervous and vascular connections, or any loss of its serous covering. Finally, although the stomach itself enlarges pretty equally in all directions, still, after filling the hypochondrium, the mobility of its bent middle directs it towards that part of the enclosing cavity where it meets with the least resistance :—namely, towards the yielding anterior wall of the belly. Hence, should the distended intestines not allow it any great descent downwards, it comes forwards; so that what was its vertical anterior surface now looks obliquely upwards ; while its inferior border touches the lower part of the wall of the epigastrium, where its artery has even been felt pulsating in very thin subjects.

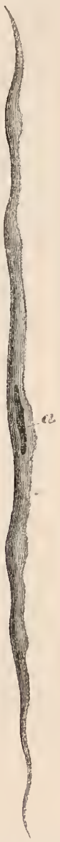
The *serous* coat of the stomach is continuous with the double laminæ of peritoneum above mentioned, which split to enclose it where they reach its various borders. Here they are very loosely connected to each other, and to the subjacent coat, by an abundance of highly elastic areolar tissue. But towards the middle of the gastric surfaces, the peritoneum, though still elastic, is closely united to the

* The muscularity of this aperture led Haller and some other anatomists to regard it as a kind of sphincter to the cardiac orifice of the stomach. But we may point out that, though the contraction of its fibres reduces the elliptical opening to a circular one, yet as this apparent constriction coincides with the descent of the diaphragm, the oblique plane of this muscle is at the same instant becoming transverse. Hence this ellipse and circle merely represent an oblique and a transverse section of the same cylinder. The diameter of the œsophagus may therefore remain unchanged.

subjacent muscular tunic. The advantage of such a yielding attachment has already been alluded to. For a description of the structure of this tunic, the reader is referred to the articles PERITONEUM and SEROUS MEMBRANES.

The *muscular* coat of the stomach consists of the unstriped or organic muscular fibre; which the researches of Koelliker have shown to consist of fibre-cells, such as are represented in *fig.* 241. The form and dimensions of these long and spindle-shaped elements vary little in the different parts of the intestine and stomach. Their length is from $\frac{1}{200}$ to $\frac{1}{100}$th of

Fig. 241.



Fibre-cell from the unstriped muscle of the intestine. Magnified about 350 *diameters.* (*After Koelliker.*)

a, nucleus.

an inch: their breadth from $\frac{1}{6000}$ to $\frac{1}{4000}$th at the middle, where they are flattened, and from whence they taper off to conical and pointed extremities. They contain a nucleus; which is from $\frac{1}{2000}$ to $\frac{1}{1000}$th of an inch in length, and about a sixth of this in breadth. Their texture is a pale substance, which generally appears to be homogeneous, but is sometimes seen to consist of a membrane* enclosing granulated or faintly striated contents. In some instances, they are marked by swellings; which, as they are rarely seen in the associated fibres, are probably due to casual local contractions of the sarcous substance itself. The arrangement of these fibre-cells is very simple; they are packed together in parallel rows (*fig.* 242.), their flattened surfaces adhering strongly

Fig. 242.

Portion of a bundle of fibre-cells from the muscular coat of the intestine. Magnified 250 *diameters.*

a, nuclei of the fibre-cells.

to each other. They thus form small and broadish bundles, between which are interposed the vessels for their supply, enclosed in a sparing quantity of areolar tissue. The union and interlacement of such fascicles of cells, builds up the large flattened strata of the muscular coat of the intestines. The fibre-cells are developed by the longitudinal extension of an oval cell; in which is deposited a special sarcous content, that soon obscures the original cell-membrane.

We shall hereafter see that these fibres surround the intestine in two layers: an external,

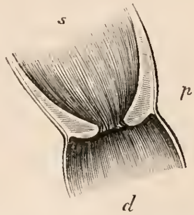
* From a comparison of very numerous observations, the author entertains no doubt that this membrane is always present, being only obscured by such circumstances as delicacy, adhesion, or refractility. In the fibre-cells of the adult human pylorus, he has often verified a distinct cell-wall or sarcolemma. And the reappearance of this membrane in the unstriped muscular fibre of the human uterus, as its cells recede or degenerate after parturition, is only one of many significant instances, that we cannot deduce the real absence of such a delicate membrane, from the mere fact of its ceasing to be visible under the microscope.

which is longitudinal: and an internal, which is circular or transverse — a general arrangement to which even the stomach forms no real exception. Before the discovery of the fibre cell by Koelliker, it was a matter of fruitless speculation, how these unstriped fibres terminated;—in other words, what was their individual length. But although this question is of course set at rest, it still remains doubtful, whether the transverse fibres of the alimentary canal return into themselves on completing one circle of the tube, or whether they take a spiral course. The latter view appears to the author much more probable. For some of their bundles often appear to join each other at a very acute angle. And whatever be the precise mechanism of their really co-ordinate contractions, it is clear that, in the longitudinal fibres, the direction and progress of contraction correspond to the axis of the cell: — that is, to the line uniting the greatest number of its sarcous particles. While it is equally obvious that, if the course of these transverse fibres were absolutely circular, the peristalsis of the whole stratum they compose would move at right angles to their axes. Such a difference in their contraction would be so unlikely, as to justify our preferring the supposition of their spiral arrangement. For this would allow of an identity in the contractions of the two strata in this respect. The course of contraction would be axial in both sets of fibres; but, *cæteris paribus*, slower (and hence apparently more local) in the far longer bundles of the transverse coils. The spiral currents hereafter alluded to as seen in the contents of the stomach perhaps strengthen this supposition.

The *longitudinal* layer of the stomach is derived from the similar tunic of the œsophagus. This, on reaching the cardia, radiates on all sides, its bundles becoming thinner as they diverge, and being gradually lost from their decussation and mixture with the various fibres they meet with. But, on the lesser curvature of the organ, they continue much more distinctly, and are often traceable as two or three broadish bundles, to within a short distance of the pylorus. The longitudinal layer which covers the pyloric extremity appears not to have any very direct continuity with the preceding. Its constituent fibres arise by scattered bundles at about the middle of the organ, and — often first uniting into two broad bands which occupy the centres of its anterior and posterior surfaces — they soon form a tubular layer, which proceeds over the pylorus, to join the commencement of the duodenum.

The *transverse* or *circular* fibres lie immediately beneath those of the longitudinal stratum; and form what is, on the whole, a thicker, if not a more uniform, layer. To the left of the cardia its rings are very few and indistinct: their places being taken by those of the third or oblique layer. But from the right of this orifice it continues towards the pylorus with a constantly increasing thickness; until finally, reaching the margin of this valve (*fig.* 243.), it is inflected towards the axis of the stomach by a rather steep and sudden curve, which presents an almost vertical surface

Fig. 243.



Longitudinal section of the alimentary canal at the junction of the stomach and duodenum, to show the thickness of the pyloric valve.

s, pyloric sac of the stomach; *d*, commencement of the first portion of the duodenum; *p*, pylorus, formed by a thickening of the transverse layer of the muscular coat of the stomach.

towards the duodenum. Those of the transverse fibres which lie nearest to the left extremity are somewhat less regularly transverse. Hence some of them decussate slightly with each other, while others, which pass downwards from the right margin of the cardia, are directed somewhat obliquely towards the left extremity of the organ.

The third or *oblique* layer lies more deeply than the two preceding, and is therefore best seen by everting and inflating the stomach, and carefully removing its mucous membrane. Where the œsophagus enters the stomach, the transverse fibres of its left margin are so close to a flattened bundle of fibres, which occupies the notch (*g*, *fig.* 240.), limiting the cardiac pouch, that the two are visibly continuous. The right or thickest part of this flattened band passes obliquely downwards towards the right side, soon breaking off from the termination of the œsophagus; and from hence it continues across the transverse layer just described, to reach the greater curvature, where the similar layers from both surfaces of the organ are reflected into each other. Its usually well-defined margin occupies — and indeed forms — the notch (*c*, *fig.* 240.). The posterior or thinner part proceeds, not only from the depression (*g*, *fig.* 240.) on the left of the cardia, but also from the neighbouring upper border of the great extremity; and its more vertical fibres are also continued downwards to the lower border of the stomach, where they meet, so as to complete the circuit of the cardiac pouch.

Movements of the stomach.—That there is an intimate connection between the œsophageal and gastric movements, is only what might be expected from that visible continuity of their muscular coats which has just been alluded to. Thus, at the close of each act of deglutition*, the lower fibres of the œsophagus contract with such force, as not only to obliterate the cardiac aperture, but even to cause the mucous membrane of this part to project into the cavity of the

* For a description of the act of deglutition see the articles "Œsophagus" and "Pharynx."

stomach.* This condition remains for some instants. And when the alimentary bolus has in this manner been impelled into the organ, it excites muscular movements.

The exact condition of the cardia during stomach digestion is scarcely known. It is obvious that the force with which it is shut must be effectively superior to the pressure exerted on the contents of the organ by the gastric contractions. Still we are ignorant how much of this force is due to the contraction of the lower œsophageal fibres, and how much to the shape, position, or structure of the stomach itself. Indeed, one cannot help conjecturing, that the decussation of the transverse and oblique fibres of the organ around the insertion of the œsophagus, might render their contractions a material assistance to the obliteration of the lower part of this tube. From the observations of Magendie†, it would seem that, during digestion, the cardia contracts tightly around a finger introduced from the stomach; and that the distention of the gastric cavity appears to regulate the intensity and duration of this closure,—so much so, that pressure by the hands, or by the diaphragm during inspiration, produces an increase of contraction. ‡ And the disappearance of this efficient closure in the dead, or even in the exhausted§ animal, suffices to show,—what indeed we might gather from its great energy,—that it is not due to mere passive contractility. Hence, on the whole, it appears preferable to regard the cardiac orifice as closed by an active muscular contraction, which is itself excited by the direct stimulus of the food that distends the stomach.

Perhaps there are few more difficult parts of our inquiry than that which relates to the precise nature of those movements which are executed by the stomach, and impressed upon the food, during its sojourn in this cavity. For the vivisection of animals has given few results; and even had they been more marked, they would scarcely have been trustworthy. The human corpse is generally diseased, or, if not, the interval after death which precedes an examination of its abdominal viscera is sufficient to remove all appearances of activity.

* Beaumont (Experiments and Observations on the Gastric Juice. Combe's Edition. 1808), pp. 62, 63., and elsewhere. Valentin, Lehrbuch der Physiologie, Band i. p. 269. Magendie, Précis élémentaire de Physiologie: Quatrième édition, vol. ii. p. 70.

† *Op. cit.* pp. 81, 82.

‡ Magendie (*loc. cit.*) and Mueller (Handbuch der Physiologie, Bd. i. p. 412) state that an alternating and rhythmical movement of the œsophagus accompanies digestion. It is independent of deglutition. The contraction of the tube coincides with the period of inspiration; and, *vice versâ*, its relaxation with expiration. But such results of vivisection cannot be safely regarded as the ordinary phenomena of the healthy body. As to how far the cardia is necessarily closed by the diaphragm in the act of inspiration, I may refer to the note to p. 309.: —to which I will only add, that any one may satisfactorily disprove its real occlusion by swallowing a bolus of food at this period.

§ Magendie, *loc. cit.*

And, finally, the results obtained from newly-killed animals on the one hand, and from Dr. Beaumont's valuable case on the other, are apparently so indefinite, or even so conflicting, that most physiologists seem content to leave the question in abeyance, until more numerous or more comparable facts afford better grounds for a decision.

A careful comparison of such results has, however, led the author to adopt the following views*, which appear to unite in one theory most of the facts hitherto ascertained respecting the muscular action of the healthy digesting stomach.

1. In the fasting state the empty stomach offers no movement whatever. This fact, which is asserted by Dr. Beaumont†, from his observations on the living human subject, may be readily verified by laying open the bellies of the domestic mammalia immediately after death. Some very slight and gradual changes in the shape of the organ, which I have once or twice noticed, form no valid exception to such a rule. This agreement in the above two classes of results is not only interesting in itself, but entitles us to lay somewhat more stress on that which follows. And it is especially useful, in that it frees us from the apprehension that any contractions which we may observe can be caused, or even greatly modified, by the air ‡ to which the dead animal's stomach is exposed.

2. At the *commencement of digestion*, or immediately after the deglutition of food, the movement of the stomach offers three varieties.

a. In some animals, a large quantity of food is often hastily swallowed, after scarcely any subdivision, far less mastication. Under these circumstances, the stomach is found closely contracted around its hard contents, sometimes even adapting its shape to that of these unyielding masses. And, as might be expected, no motion is discernible.§

b. Dr. Beaumont narrates the opposite effect of a very small quantity of liquid food in the human subject. It excites a vermicular action, a gentle contraction or grasping motion of the stomach, so that the wrinkles of the

* These will be found in an Essay which, written in 1847, was published in the "Medical Gazette" for 1849.

† Beaumont, at p. 105. expressly; at pp. 23. 57., by implication.

‡ Though, by the bye, as this would chiefly cause irregular motions, it would rather oppose, than produce, any uniform and constant movement. The effect of air on the intestine is alluded to hereafter.

§ This condition, which is frequent in the domestic Carnivora, appears to be usual in the Rabbit, in whom it is often kept up by the comparatively unyielding nature of the food. In such a case the contents of the stomach are dissolved, as it were, from without inwards, in successive strata; which are slowly and constantly stripped off by the muscular action, and squeezed through the pylorus. In all these instances I have found the movements of the organ much less marked than where the food was present in a smaller quantity and a state of greater subdivision. And in the Rabbit, both the stomach and intestine appear to be unusually sluggish; as shown by the feeble movements of the former during digestion, and of the latter under the magneto-electric stimulus.

mucous membrane gently close upon it, and gradually diffuse it over the whole surface.*

c. The ordinary state of the human stomach during the digestive act lies between these two extremes; and may be defined as one of moderate distention, with food which has been subdivided by mastication, and diluted with saliva and gastric juice, so as to possess a pulpy or semi-fluid consistence.

In attempting to imitate this condition in the Dog, I have found it best to choose an aliment which already possesses a pultaceous or semi-liquid consistence,—such as a thick soup,—and to administer it in large, but not excessive quantity. On pithing the animal a quarter of an hour afterwards, the following movements are seen. The most noticeable is a peristalsis or transverse constriction, which sets out from the cardiac extremity, and travels slowly towards the pylorus. It is comparatively feeble until it reaches the junction of the pyloric two-fifths, and the cardiac three-fifths of the organ. Here it suddenly becomes much more distinct; and from hence continues rapidly forwards, as a well-marked circular depression, until it reaches the pylorus. Having arrived there, an interval of relaxation succeeds, and is followed by the recurrence of a similar contraction. As nearly as can be judged, the average period of relaxation is about one minute, and the contraction itself occupies nearly the same time. Cotemporaneous with this contraction there is a certain amount of longitudinal shortening of the organ. The pyloric orifice is always firmly shut.

In the interior of the human stomach, Dr. Beaumont could only verify an alternate contraction and relaxation; a vermicular action of the transverse fibres, and a shortening produced by the longitudinal coat. The exact details of this occurrence he could not follow. He also noticed a constant agitation of the organ produced by the respiratory muscles.† But Dr. Todd and Mr. Bowman ‡ have mentioned a case, in which the vermicular actions of a distended stomach were distinctly seen through the wall of the belly during life.

So far as this imperfect evidence goes, it is evidently favourable to the view, that the muscular contraction of the human stomach during this stage of digestion is similar to that seen in the newly-killed animal.

It is therefore our next object to inquire — (1) What are the movements which such a peristalsis would necessarily impress upon the food? And (2) how far do they correspond with those which have been actually observed?

(1.) The effect of peristalsis in a closed and distended tube may be represented by an inflexible hollow cylinder, filled with liquid, and accurately fitted with a perforated septum (*b*, *fig*. 244.), which is capable of free movement along its interior. Let such a septum be moved in either direction, and it at once exerts a pressure on the body of liquid (*c*) contained in that end (*a*) towards which its motion sets. The pressure being equal in all directions, a portion of the fluid escapes backwards through its aperture (*d*). This retrograde course is, *pro tanto*, a current; and one which will be continually lengthened by the advance of the septum along the remainder of the tube. And the slow successive movement of a series of such septa would establish two continuous currents in the liquid; a peripheral of advance, and a central of return.*

Fig. 244.

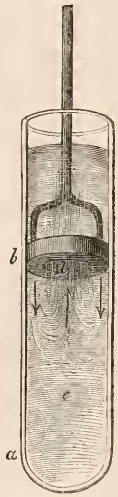


Diagram to illustrate the effects of peristalsis in a closed tube containing liquid.

a, Closed end of the tube; *b*, perforated septum, moved towards *a*, and causing the peripheral currents indicated by the arrows, in the same direction; *c*, quiescent mass of liquid, giving origin to *d*; *d*, central current, prolonged from the corresponding arrow, and passing through the perforated septum.

The existence of two such currents would be little affected by the membranous nature or peculiar shape of the human stomach. Even comparative inactivity of the cardiac pouch would not prevent their occurrence, as a consequence of pyloric peristalsis. While very moderate contractions of this sluggish part would accurately define the axis and its cur-

* Condensed, in Dr. Beaumont's own words, from pp. 62, 63. 96, 97, of his work. This activity of the rugæ themselves may remind us of their inherent muscularity (see p. 325. of this article).

† Probably much exaggerated, if not chiefly produced, by the adhesion of St. Martin's stomach to the wall of his chest.

‡ Todd and Bowman's Physiological Anatomy, vol. ii. p. 196.

* The following description so well supplies the interval between such a model tube and the human stomach, that I cannot refrain from quoting it. "The muscular action of a fish's stomach consists of vermicular contractions, creeping slowly in continuous succession from the cardia to the pylorus, and impressing a twofold gyratory motion on the contents; so that, while some portions are proceeding to the pylorus, others are returning towards the cardia." (Owen's Hunterian Lectures, vol. ii. p. 236.).

rent, as that curved line which unites the cardiac and pyloric apertures (*a, fig.* 245.).

Fig. 245.

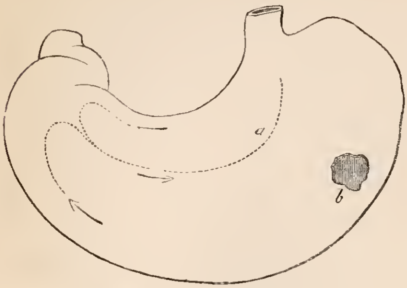


Diagram to show the general direction of movement impressed on the semifluid food in the digesting stomach.

a, real axis of the stomach, uniting its cardiac and pyloric apertures; *b*, situation of the abnormal opening in St. Martin's case. (The arrows correspond to the peripherial current of advance, which is effected by peristalsis; and the central current of return, which is reflected from the preceding at the pylorus.)

(2.) The observations of Dr. Beaumont are as follows* :—" The bolus, as it enters the cardia, turns to the left, passes the aperture, descends into the splenic extremity, and follows the great curvature towards the pyloric end. It then returns in the course of the smaller curvature, makes its appearance again at the aperture in its descent into the great curvature, to perform similar revolutions. These revolutions are completed in from one to three minutes; the bulb of the thermometer invariably indicates the same movements." He is careful to add, that there is an admixture of the ingesta, which implies that the movement is not simply a revolution; for that, if this were the case, "the central portions would retain their situation, until the outer or chymified part had passed into the duodenum."†

Now in order to render the movement thus observed perfectly compatible with that above deduced, we have but to recollect the situation of the aperture from which the inspection of St. Martin's stomach was made. This was at the left extremity of the organ (*b, fig.* 245.). Whence it is obvious, that any backward movement along the real axis (*a*), connecting the two orifices of the stomach, would be so near to the superior curved border, and so far from the point of view, that Dr. Beaumont could scarcely have avoided imputing to it the course which he has done. While, since every part of the stomach would be occupied by one or other of the two currents, the mutual interference of these at their borders must gradually cause an uniform diffusion of the various alimentary matters moving with them. And finally, the reflection of one current into the other at the pylorus, insures an equal contact of all the semifluid food with the surface of the mucous membrane; since those portions of the ingesta which occupy the axis of the stomach during one moment, are destined to move along its periphery during the next.

3. In the *later stage of digestion*, the movement seen in the Dog's stomach soon after death differs from the preceding.

The cardiac extremity appears even less active than before; and the longitudinal shortening of the organ is also less marked. The chief visible commencement of contraction is at the same place where it was formerly increased, and where it now forms a deep constriction or hour-glass contraction. After this constriction has continued a short time, it sends onwards towards the pylorus a rapid peristalsis, which appears nearly to obliterate the tube in its course, and ends by engaging the muscular ring of this valve. A slight relaxation closely follows this peristalsis; and is succeeded by a complete dilatation of the pyloric sac. Lastly, the hourglass contraction itself sometimes disappears; and an interval of about two minutes precedes the repetition of the whole process. Often, however, the constriction remains until the peristalsis recommences.

Dr. Beaumont's observations* again seem to supply the counterpart to this description. He states that, when chymification has advanced, the motion is quicker. And on attempting to pass a thermometer tube towards the pylorus, it is stopped by a stricture†, which is situated about three or four inches from this aperture. A forcible contraction is first perceived; but in a short time, there is a gentle relaxation, when the bulb passes without difficulty, and is then drawn forcibly towards the pyloric end for three or four inches. It is then released, and forced back with a spiral motion for the same distance, when it seems to be again obstructed by the stricture. But if pulled up through this, it moves freely in the cardiac portion, mostly inclining towards the splenic extremity. The repetition of the contraction is preceded by an interval of about three minutes, during which the food revolves as in the previous stage.

It is scarcely necessary to point out, that when the almost obliterated pyloric tube is filled by the tightly grasped thermometer bulb, no axial current can possibly be produced by the peristalsis. The pylorus having contracted, and its pouch relaxed, the contractility of the whole organ would determine a rush of fluid around the bulb; and this would be reflected from the valve into the axis of the

* *Op. cit.* p. 101.

† This admixture he ascribes to a triturating or agitating motion, which is partly gastric, partly respiratory. But the existence of the circulating movement described sufficiently proves that this mixture was inherent to the process, and not (as his supposition would imply) a result of its disturbance.

* *Op. cit.* pp. 102. 104.

† The similar narrowing seen in the digesting stomach of animals has been called the "transverse band"; a term which is objectionable, inasmuch as it implies the presence of a special structure that does not really exist.

tube. We should thus get two currents, which, at least in situation, would be identical with those produced by the peristalsis of the succeeding interval.

Action of the pylorus.—The structure of the pylorus (πυλωρὸς, *portæ custos*) has already been described. As regards its action, it is obviously the sphincter of the stomach. As such, it has been supposed to possess a kind of selective power; by virtue of which it contracts against the food in the earlier stage of digestion, but subsequently relaxes to permit the passage of the chyme. This view, however, appears to me very doubtful.

In the empty stomach, the pylorus is generally open, and readily * allows of the passage of bile from the duodenum. In the early stage of digestion, it is firmly shut; and retains the contents of the organ against gravity, or even against such a manual pressure as readily expels them from the cardia.

But just as in the second stage of gastric digestion, it is plain that the valve does not undergo any sudden or great relaxation,—for such would allow the passage of a large quantity of the moving and semifluid food, much of which would be still crude and undigested — so the very gradual diminution†, noticed by Beaumont in the early stage, renders his inference,—that, even from the first, chyme is constantly passing into the duodenum— very probably correct. ‡ Supposing this to be the case, it is evident that the action of the pylorus must be very similar at both these periods. And after numerous and careful observations on this part of the Dog's stomach towards the close of its digestive act, I have never yet been able to substantiate any definite relaxation of the pylorus; or any but an inconsiderable oozing of chyme at the time of that active peristalsis which has been described above. Hence I prefer to regard the passage of the chyme as produced by that great increase of force which the contractions of the pyloric sac acquire at this period;—a cause which appears so sufficient, that it seems scarcely justifiable to assume any additional one. The supposed relaxation of the pylorus seems also contradicted by a remark of Beaumont's, that, even at the end of the process, when the passage of chyme is greatly accelerated, the above contractions still continue.

In short, instead of a relaxed pylorus, through which a moderate peristalsis urges a selected portion of the food, it appears the state of this aperture during the close of gastric digestion is that of a contracted valve, through which the tolerably uniform chyme is being strained in small quantities, at frequent intervals, by a comparatively violent muscular contraction.* Hence the separation of the chyme from the other contents of the stomach seems to be effected by a process somewhat analogous to a coarse filtration, aided by pressure.

How little the pylorus could reject the "crude" portions of the tolerably homogeneous chyme, to transmit its more fluid or dissolved constituents, is shown by the facility with which indigestible substances of various shapes and sizes pass into the duodenum. Of these we can only say, that it is probable they are generally carried through the constricted pyloric sac and valve by a very forcible peristalsis.† The weight and solidity of many such masses allow them to remain some time in the cardiac pouch, perhaps lodged behind the transverse constriction which separates this from the pyloric sac. Both of these circumstances often defer their passage to the later stage of digestion. Smaller substances, however, sometimes traverse the whole canal in so short ‡ a space of time, that it is difficult to avoid believing that they leave the stomach very shortly after entering it.

But while we may thus regard the pyloric valve as exerting but one and the same action during the whole period of gastric digestion, we shall find it difficult to substitute any other theory of its action for that local appreciation or selection which we have attempted to refute. Its contraction is accompanied by that of the whole muscular coat of the stomach; of which the pylorus forms, apparently, but a terminal thickening. And of the only two other facts which are cotemporaneous in their occurrence and duration — viz., the presence of food, and of gastric juice — the first affords little explanation; while the second is more likely to be another effect of the cause, whatever it may be, which excites that co-ordinate muscular action in which the pylorus appears to play an important, though simple, part.

It is interesting to observe how little the action of the pylorus is connected with any stimulus other than a gastric one. The flow of bile into the fasting stomach may perhaps be regarded as a passage, such as this janitor might well concede to a fluid which is not only harmless, but recrementitious. But in

* Bile is almost always found in the empty stomach of Dogs and Cats. (Compare Beaumont, pp. 86, 87.)

† The diminution due to absorption would probably be at first compensated by the addition of gastric juice.

‡ According to Magendie (*Op. cit.* p. 91.), the pylorus of the Horse is always found open, and is probably relaxed during life. It is only thus one can explain the well-known fact, that the quantity of food taken by this animal at an ordinary meal has a bulk which amounts to four or five times that of its distended stomach. Indeed, water has been found in its cæcum six minutes after being swallowed. (Coleman in Abernethy's Physiological Lectures, p. 180.)

* It is scarcely necessary to add, that the mechanism of such an act does not require that the cardia should be, however momentarily, the stronger valve of the two. For the force of an obliterating peristalsis would be at first almost spent upon the pylorus towards which it sets. While that of a weaker contraction would be chiefly expended upon the pyloric sac. And the residual force of both would chiefly dilate the yielding and quiescent large extremity.

† A peristalsis, the energy of which it is probable that they themselves increase.

‡ Thus the author has known peas traverse the canal in two hours.

the obstructed canal, fæces pass through it from the duodenum with equal facility, although the stomach soon resents their presence by vomiting;—an act which seems generally to imply a shut pylorus. And Magendie* has observed, that the gases of this upper portion of the intestine can be made to pass the valve with equal facility; while those distending the stomach excite its contraction.

Under ordinary circumstances, whatever be the period during which the contents of the stomach sojourn in its cavity, or the movements they experience at this time, they are finally propelled onwards into the duodenum.

Sometimes, however, they take a backward course; and pass through the œsophagus, to re-enter the mouth, and be expelled from this cavity. Such a reversal of their normal direction occurs in the acts of eructation, regurgitation, and vomiting. These acts, however they may differ in their details, must (*à priori*) agree in the conditions of their occurrence. They require a relaxation of the cardia, a closure† of the pylorus, and a compression of the stomach. The latter of these three requirements may either be the result of the contractions of the organ itself, or may be effected by an external or independent pressure.

In simple *eructation* or belching, part of the gaseous contents of the stomach are ejected from the mouth. This act generally occurs towards the close of digestion, and in dyspeptic individuals; the quantities of gas thus evolved being often very considerable. In what way the cardia is opened, or how far the evolution of large quantities of these aëriform fluids in the stomach may not contribute to render it patulous, is at present very doubtful. But the intermittent character of the occurrence certainly looks unlike a mere leakage of an aëriform fluid. While the frequency with which the human stomach contains gases, and the completeness with which the cardia resists their expulsion in vivisected animals‡, increase the difficulty of such a supposition, and, so far, tend to confirm that of a temporary relaxation of this aperture. The direct agent of the expulsive act seems equally uncertain. The contractions of the stomach seem quite sufficient to account for it. And there is certainly no violent abdominal pressure. But such mobile fluids would scarce require a remarkable effort. While, as far as can be judged, the act appears to coincide with the period of expiration.

An examination of that voluntary eructation which most persons can accomplish, may perhaps strengthen the conjecture, that some slight abdominal pressure is a constituent of the ordinary act. Here, by a kind of twitching* action of the œsophagus, which is accompanied by a sensation that is referred to the upper portion of this tube, air is introduced into its interior; and is then expelled, with a considerable sound, by a well-marked movement of expiration, during which the glottis appears to be at least partially closed. And the expulsion of the air artificially introduced is often accompanied by that of a portion which was previously contained in the stomach itself. So that involuntary and voluntary eructation may be said to merge into each other.†

In the act of *regurgitation*, more or less of the liquid contents of the stomach are returned into the mouth. This act closely resembles the preceding, of which it often appears to be an accidental complication; — a small portion of liquid being carried upwards, along with an eructation of gas. In other instances, however, the liquid is unaccompanied by elastic fluid; and rises so quietly, that it is only perceived on reaching the fauces and back of the tongue, where its acid taste causes it to be at once recognized. It is probable that the process which effects this expulsion is similar to that of eructation. If we could conjecture any difference, it would be, that the abdominal pressure plays a less important part.

The act of *vomiting* differs from both of the preceding: not only in the miscellaneous character of the matters which it can expel from the stomach, and in the greater energy with which it is effected; but also in the fact, that a pressure extrinsic to the organ itself here forms what is, at any rate, the chief agent of the process.

This abdominal pressure, which has been before alluded to, we shall now proceed to describe.

In those ordinary movements of respiration which are executed chiefly by the diaphragm and abdominal muscles, the bulk or capacity of the belly is little affected. For during the act of inspiration, the descent or contraction of the former, exactly coincides with the relaxation of the latter muscular structures; while during that of expiration, the compression which these exercise is neutralized by the recession or ascent of the now relaxed diaphragm. Hence the moveable viscera of the belly themselves evade all pressure; and merely transfer a very slight force from the anterior to the upper wall of the cavity, or *vice versâ*. But if, while the diaphragm remains depressed and contracted, the abdo-

* *Op. cit.* p. 83.

† Of course this closure need only be comparative: that is, the mere resistance of the contents of the stomach to compression would suffice to determine their passage through the more relaxed of its two orifices.

‡ As in Magendie's observations, elsewhere alluded to.

* This is often called a deglutition of air, although the movement is utterly unlike that of swallowing.

† Thus the dyspeptic poor who crowd the out-patient rooms of hospitals, sometimes eructate so voluntarily, and even ostentatiously, that the act really seems to be done, not so much to expel gas from an over-distended stomach—as to attract commiseration. And it is said that, in polite Chinese circles, a chorus of eructations at the end of a banquet formally acquaints the host with the repletion of his grateful guests.

minal muscles be also brought into vigorous action, the whole force of either of these two muscular strata may be regarded as compressing the viscera within the abdominal cavity. And since many of these viscera are hollow organs, which enclose moveable contents, and communicate with the exterior of the body, such a forcible pressure will expel the contents from their interior, so soon as their terminal orifices are thrown open; — whether by their relaxing spontaneously, or yielding to any superior force. In this way, the contraction of the walls of the belly plays an important part in the acts of defæcation, micturition, and parturition, as well as in that of vomiting.

Now in the three former of these acts, the intermittent abdominal pressure does but assist those more continuous expulsive contractions which are effected by the muscular walls of the hollow viscera themselves. And supposing that the cardia were open, and the pylorus shut, it is obvious that either pressure on the stomach, or contraction of its walls, would alike tend to expel its contents.

Careful observation of the act of vomiting in any of the higher animals will show that it is always assisted by the abdominal pressure. And the vivisections which many experimenters have practised, agree in carrying this investigation further; and in stating, that this pressure, which ordinarily results from simultaneous contractions of the diaphragm and abdominal muscles, may be due solely to the latter *, (as is normally the case in Birds †), or to the former, or even to an inconsiderable compression exerted by the lower ribs upon the epigastric region.‡ While the solitary observation of Maingault §, which affirms the occurrence of vomiting in the absence of all such pressure, stands expressly contradicted by the Committee of the French Academy appointed to report upon his Memoir.

But whether the stomach really contracts during the act of vomiting, — and if so, what is the amount of assistance which it thus affords this process,—are questions which, long the object of physiological controversy, can even now scarcely be regarded as decided.

On the one hand, there are not wanting experiments, which show that the act of vomiting may be effected without the aid of any gastric contractions whatever. Among such we may specially adduce the vivisection practised by Magendie ‖, in which a Pig's bladder was substituted for the stomach of a living Dog, and was subsequently emptied, by vomiting, of a large part of its contents. Such a result conclusively proves that gastric contractions are not essential to the physical act of vomiting, however frequently they may take a part in the process. And

* Magendie, Sur le Vomissement, pp. 22. 37, 38.

† Krimer in Horn and Nasse's Archiv. 1816.

‡ Bulletin de la Faculté de Médecine, 1813, No. 10. p. 481. et seq.

§ Sur le Vomissement. Paris, 1813.

‖ *Op. cit.* p. 18.

that inactivity of the stomach, which has been directly observed by many * physiologists in the artificial vomiting of vivisected animals, has been all but actually seen in the living human † subject.

On the other hand, the observations in which a muscular contraction of the stomach has been seen to concur in this act, are even more numerous than the preceding. The amount of such contraction seen appears to have varied, having sometimes been so slight as to be scarcely visible. In all instances, it has specially engaged the pyloric extremity of the organ: and, in most, it is described as either circular‡, and alternating with relaxation; or peristaltic, like that found in the digesting stomach, independently of all vomiting. And though an anti-peristaltic movement is detailed by Haller and others, yet so far as I can find, this doctrine, which is expressly contradicted by the observations just referred to, rests only on one or two § vague descriptions of Wepfer, Rudbeck, and Schwartz.

From these very brief allusions to both sides of this conflicted question, the author has been careful to eliminate every statement which does not refer to actual facts. And the reader must recollect, that not only does the stomach offer few obstacles to such direct observations ‖, but that some of those summed up in the above statements, are rendered additionally trustworthy by being results quite at variance with the theories of their observers; while others have been confirmed by very frequent and careful repetition.¶

Hence, on the whole, I think we must conclude as follows: — The act of vomiting is essentially, and perhaps sometimes solely, the result of powerful abdominal pressure on the contents of the stomach. It implies a patulous cardia. The abdominal pressure which effects it, often coincides with, and is aided

* Bayle, Wepfer, Chirac, Baciaccus, Senac, Schwartz, and (especially) Magendie.

† Lépine, Bulletin de l'Academie de Médecine, vol. ix. p. 146. In this case, which has been strangely misquoted by many English authors, the stomach was protruded from a wound in the belly. It contained food and air, remained quite motionless, and could not even be excited to contract by manual titillation and pressure. But as soon as it was returned into the cavity of the belly, the abdominal efforts at vomiting, which had been previously ineffectual, discharged its contents.

‡ Haller, Opera Minora, vol. i. p. 389.; Schwartz, in Haller's Disp. Anat. vol. i. p. 327.; Wepfer, Sur la Cigue aquatique, p. 253.; the Author, *Op. cit.* p. 11.; Betz, Wurtemberger Corr. Blatt. Bd. xx. pp. 145. et seq.

§ Rudbeck, quoted by Morgenbesser in Haller's Disputationes Anatomicæ, vol. i. p. 293.; Wepfer, *Op. cit.* 251. and elsewhere; Schwartz, *loc. cit.* Rudbeck describes it as a contraction, which began at the pylorus, and was followed by a systole of the whole organ, from the lower to the upper orifice. While, according to Wepfer, it commenced in the duodenum, and passed hence towards the pylorus and the middle of the stomach.

‖ See remarks on the gastric movements, p. 312.

¶ Although unable to quote exactly, I believe Magendie somewhere alludes to his own results as confirmed by the vivisection of about two hundred animals.

by, a contraction of the muscular coat of the stomach itself. But there is no sufficient reason for supposing that an anti-peristalsis ever obtains, far less for imagining that it constitutes a special element of this expulsive process.

We may, perhaps, find some corroboration of this statement in the circumstances which constitute, so to speak, the *juvantia* and *lædentia* of this complex act. Perhaps the easiest variety of vomiting is that which frequently occurs in the sucking child. Here it is probable that three conditions, each of which might have some influence in facilitating the return of food, are all present at once: — namely, a distended stomach, an active gastric movement, and the peculiar form of deglutition which continuous sucking would imply.* The first of these three circumstances would mainly act by affording a greater resistance to the abdominal pressure; which although probably reduced to a minimum, is no doubt necessary to the process. And the second may perhaps constitute one of the chief occasions of this regurgitation, by impelling the contents of the stomach through the cardiac orifice. While the latter aperture might be thrown open by some slight and accidental † irregularity in the act of deglutition.

These conjectures are strengthened by the observation, that distention of the stomach, from any cause whatever, appears greatly to facilitate the occurrence of vomiting. That experience of this act, which a sea-voyage affords, may suffice to recall to most readers how much more easily the process goes on in a moderately full stomach than in an empty one. It is for the same reason that copious draughts of water are used to assist the action of emetics. And during the vomiting of both Man ‡ and animals §, the stomach is often gradually distended with air by a series of involuntary "retchings," which thus probably afford a similar assistance to the process. ‖ In like manner, it is to that distention of the whole belly which intestinal obstruction produces, that we must ascribe the peculiarly easy character of the vomiting that is then set up. The easy vomiting which occurs in cases of pyrosis may be similarly explained.

In addition to these mechanical elements of the process of vomiting, there are others which, though less constant, must not be overlooked. For not only do they take a frequent share in the phenomena of this act, but they also remarkably indicate its co-ordinate nature and arrangement. Thus the act is generally ushered in by a feeling of indistinct uneasiness, distention, or even pain, in the gastric region; which is often attended by an increased secretion of saliva, and a loathing of food, that is soon heightened into positive nausea. This is shortly followed by giddiness, dimness of sight, and languor: — symptoms which are evidently of cerebral origin. Next occur the retchings, or efforts at vomiting, before alluded to; which are probably irregular movements of the œsophagus, unaccompanied by abdominal pressure. Where the stomach is but little distended with fluid, these movements often seem to favour the subsequent occurrence of vomiting, by filling the organ with air. Finally, an uncontrollable effort so far reverses the ordinary action of the muscles of respiration, as to bring into one period contractions which usually occupy different and alternate times. An energetic closure of the glottis follows the descent of the diaphragm; so that this muscular septum is fixed by the distention of the thorax, as well as by the contraction of its own fibres. And the abdominal muscles now contract violently upon the stomach. During each actual effort of vomiting, the compression which is exercised by the muscles of the trunk causes the head to become greatly congested; so that the features are red and swollen, and the large veins of the face and temples visibly dilated. The pulse is also quickened; and the skin often rises in temperature, and perspires. The expulsion of the contents of the stomach from its cavity is sometimes attended by great pain, which is referred to the lower part of the œsophagus. And in spite of what is apparently a tolerable (though reversed) imitation of the movements of deglutition, a good deal of liquid generally eludes the curtain of the soft palate, and gushes through the respiratory channel formed by the nasal fossæ and nostrils. The subsequent phenomena mainly depend on the origin of the vomiting. Where, as is often the case, its immediate cause is removed by the expulsive act itself, the patient soon recovers his normal condition.

A proper consideration of the various causes of vomiting would belong rather to a medical than to a physiological treatise. We need but point out that they may all be divided into two classes:—(1) those in which there is an irritation of the nervous centre itself; and (2) those in which an irritation, applied to the nervous periphery, is transmitted thence to the centre, from whence it is reflected into the various organs which constitute the agents of the expulsive process. As examples of the first class, we may adduce the frequent instances in which vomiting accompanies a cerebral injury * or disease. As

* Schultz and Salbach (Valentin's Lehrbuch, vol. i. p. 281.) seek to explain the vomiting of infants by the peculiar form of the stomach at this age. But comparative anatomy entitles us to doubt whether the mere absence of a cardiac pouch would imply such a result. And I believe that their description somewhat exaggerates this peculiarity. For the stomach of the mature fœtus often has a cardiac extremity not much less projecting than that of the adult.

† Compare Beaumont, p. 62.

‡ Lépine, *loc. cit.*

§ Magendie, *loc. cit.*

‖ This so-called deglutition of air has a close resemblance to that which precedes voluntary eructation. Its chief conditions seem to be, a spasmodic action of the œsophagus, and a patulous cardia.

* To such centric irritations might also be referred that kind of vomiting which sometimes results from

instances of the second, we might adduce, not only that ordinary form of vomiting which is brought about by a direct irritation of the stomach itself, but those numerous cases in which it follows the application of various stimuli to similar or different parts. Such are mechanical irritations of the soft palate, intestines, or peritoneum; disgusting smells, sights, or sounds; prolonged immersion in cold water; or even wounds of the extremities.

The path by which these several kinds of peripheral irritation reach the nervous centre probably varies in different cases. Where they are mechanical, it is obvious that they are conducted to the central organ by the afferent or sensitive nerves upon which they impinge. Thus, as regards the stomach itself, irritation or section of the pneumogastric or splanchnic nerve often produces vomiting. But some emetic substances, such as antimony*, are equally active when introduced into the blood. And Magendie's experiment † shows that — whether the poisoned current of this fluid generally exerts a local action upon the stomach or not — it is to its influence upon the nervous centres that the act of vomiting must mainly be referred. The various constituent phenomena of the process sufficiently indicate the medulla oblongata as that segment of the cerebro-spinal centre in which the reflection towards the periphery occurs. But the ensuing movement is by no means a simple reflex action. On the contrary, the number of organs linked together to produce it, and the alteration in their ordinary times, modes, and degrees of activity which they exhibit, render the whole process so complex, so truly coordinate, that, far from limiting our attention to the mere reflex course which its exciting cause sometimes takes, we ought rather to regard vomiting as an involuntary or physical nervous action of the highest order. The sensations that have been noticed as accompanying it seem probably due to the cognizance taken by different organs, of changes which are perhaps themselves motor. At any rate, we are hardly justified in classifying them along with the "reflex sensations" sometimes met with in disease.

In some instances, a curious variety of the process of vomiting seems to return different parts of the gastric contents at different intervals of time; — the expulsion of more fluid and digested portions being followed, after the lapse of a considerable period, by that of crude and undigested masses of food. A small number of such cases perhaps depend on a peculiar hour-glass shape of the organ, aided by a casual constriction due to its muscular coat: — conditions which might unite to isolate a part of the contents of the organ for a longer or shorter period. But most of them might probably be explained by the weight, bulk, and situation of the alimentary masses in the organ; and by the other mechanical circumstances which favour or impede the act of vomiting itself.

The last efforts of a prolonged vomiting often bring up a quantity of bile. But from what has already been stated, it is evident, that during the intervals of energetic vomiting, a portion of the duodenal contents may easily find their way into the stomach, and be subsequently expelled thence. Indeed, it may be doubted whether the pylorus is completely occluded at the moment of the expulsive act: — especially in those cases in which the intestines are themselves distended with fluids exposed to the same violent pressure as the contents of the gastric cavity.

Rumination.— There are certain individuals who are capable of returning, at will, a greater or smaller portion of the contents of the digesting stomach into the cavity of the mouth. This act has received the name of *rumination*, from its analogy to the ruminant process which forms a stage in the normal digestion of some animals. Like the latter, it is a voluntary return of the undigested food, which is often followed by a re-mastication of its more solid portions. Apart from its voluntary character, it might be regarded in either of two points of view :—as a more complete form of regurgitation; or as a peculiar variety of vomiting, akin to that seen in infants, and, like it, especially distinguished by the absence of nausea and of constitutional disturbance.

The mechanism of the process appears to be precisely what these analogies would imply. A very deep inspiration is followed by a voluntary contraction of the abdominal muscles; and, after a moment during which the trunk is kept motionless, the food rises into the mouth.* From hence, after more or less mastication, it is again swallowed in the ordinary way. The abdominal contraction sometimes requires to be aided by manual pressure in the gastric region. The date and duration of the act, as well as the frequency with which it is repeated, vary greatly in different cases.

The precise share taken by the stomach itself in this rumination seems just as obscure — and is probably as variable — as that by which it assists in the act of vomiting.

In many instances an examination of the organ after death has shown no peculiarity of

purely mental emotion, and which is typified in the exaggerated phrase of "being *sick*" of any thing or topic.

* With respect to the vomiting produced by tartar-emetic, the author has made an observation which tends to show that, whatever the mechanical share taken by the stomach itself in the act, this organ does, in some instances, effect such a local secretion of the emetic from the blood into the gastric cavity, as may tend to remove the drug from the system. On injecting a solution of tartar-emetic into the superficial femoral vein of a dog, the mineral was found ten minutes afterwards in the fluid contents of the animal's (digesting) stomach, in a state of concentration much exceeding that in which it must have been mixed with the mass of the blood. And there seem to be reasons for conjecturing that a similar local secretion occurs in the case of the salts of some other metals; and, probably, of ipecacuan.

† Quoted at p. 317.

* Magendie's Physiologie, tome ii. p. 152.

its muscular coats *; in others, the œsophagus has been found greatly thickened; and in others †, this thickening has also implicated the stomach itself. In other cases ‡, this organ has been found with a narrowed or hardened pyloric sac, or a dilated and relaxed cardiac extremity or aperture; or even in a state of suppuration. From a comparison of these appearances, it would therefore seem, that the act is often at least assisted by vigorous gastric movements. And the existence of such movements is also implied by the fact, that this rumination occurs at the period of digestion, when the organ is distended, and its pyloric aperture shut.

As regards the main feature of the process—namely, its subjection to the will, — it is important to notice that great variations obtain. Thus, in some of these cases, the expulsion of the food has required a violent effort. In the majority, it has been easily evoked or suppressed. While in others, it has been almost uncontrollable; or its non-occurrence at the habitual time has been followed by a painful feeling of fulness, or by the act of vomiting.

On the whole, the variable condition of the stomach itself, the slow acquisition of the habit in some subjects, its close resemblance to the easy vomiting of young children, as well as its analogy to voluntary eructation — all these circumstances favour the belief, that the unusual effort of volition which forms the main feature of the act has for its object to open or relax the cardiac orifice and the lower part of the œsophagus. Without such a relaxation, any further efforts on the part of the active pyloric sac would be inefficient: while, with it, their place might be more than supplied by the presence of powerful abdominal contractions. Finally, it is much more consistent with all we know of these two segments of the alimentary canal to suppose the œsophagus capable of being slightly affected by a voluntary effort, than to imagine any part of the stomach placed in the anomalous position of a powerful voluntary muscle, its muscular coat sometimes remaining unaffected, sometimes being positively disorganized by structural disease. And the hypertrophy of the gastric coats, in some of the instances before alluded to, may be interpreted as the effect of rumination, quite as much as its cause; in other words, as being possibly produced by that prolonged gastric movement which would result from such an act, in those instances in which the organ was otherwise healthy.

Mucous membrane.— The mucous membrane, on which the functions of the various parts of the intestinal canal essentially depend, is so modified in the stomach, as to offer a complex arrangement, such as remarkably contrasts it with the simpler layer that lines the upper part of the tube.* And it is distinguished from the compound membrane of the intestine by the possession of certain special structures :—namely, the proper gastric cells, or glandular epithelia, as they are sometimes called.

The remaining histological constituents of this mucous membrane are similar to those met with in other parts of the canal. A delicate membrane is variously involuted or moulded upon a quantity of areolar tissue. The latter texture, which is thus immediately subjacent to this "basement" membrane, forms the matrix of the mucous coat, and, as such, contains its vessels, nerves, and lymphatics, and connects it with the middle or muscular coat. While on its opposite side, the delicate limitary membrane sustains a number of minute cells, that bound the cavity of the tube.

Examined by the naked eye *in sitû*, the mucous membrane of the stomach is seen to be a tolerably firm but soft layer, of a pale pink colour, which everywhere loosely lines the interior of the muscular coat, and projects from its surface in numerous wrinkled folds. These *rugæ* chiefly occupy the cardiac half of the organ, forming convolutions which, though somewhat irregular, are mainly longitudinal. They are effaced by distention of the stomach. And on putting the mucous membrane on the stretch, we may often discern that its whole internal surface is occupied by extremely minute pits or depressions †; the confluent and projecting intervals of which become so much longer as they near the pylorus, that they may almost be compared to very short and scattered villi. These depressions are the openings of the stomach-tubes or proper gastric glands.

The *stomach-tubes* (*c*, *a*, *d*, *fig.* 246.) may be described as cylinders of basement membrane: which are packed vertically side by side in a sparing matrix of dense areolar tissue, and are filled by a peculiar cell-growth. Below, they terminate in closed and rounded extremities (*d*). Above, they expand slightly before reaching the free surface of the membrane, where their margins finally become continuous with each other, so as to form a series of low ridges, the height and width of which vary somewhat in different parts of the stomach. The length of these tubes is, on an average, about $\frac{1}{25}$th of an inch. But this estimate, which is tolerably accurate as regards the middle of the organ, may be almost doubled for the pyloric, and halved for the cardiac region, — a difference which forms the main cause of the very different thickness of the mucous membrane in these two parts.

* Voigtel. Path. Anat. vol. ii. p. 517.

† Arnold's Untersuchungen. Zurich, 1838, p. 211.; Valentin's Lehrbuch, vol. i. p. 273.

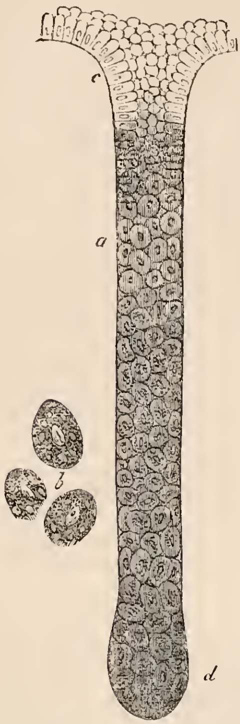
‡ Arnold. Lehrbuch der Pathologischen Physiologie, § 571.

* See articles Mouth, Œsophagus, and Pharynx.

† Such details may be best verified by everting and inflating a perfectly fresh stomach; and removing the adherent mucus by pouring on it a very gentle stream of water, from a gradually increasing elevation.

Their diameter is about $\frac{1}{350}$th of an inch, but is also increased towards the pylorus. Thus their length has to their breadth a pro-

Fig. 246.



Stomach-tube from the middle of the human stomach. Magnified 140 *diameters.*

a, wall of the tube, lined with large oval nucleated cells; *b*, the same oval cells isolated, and magnified 800 diameters; *c*, nucleated cells of columnar epithelium, occupying the upper parts of the tubes, and the intervening ridges; *d*, blind extremity of the tube.

portion of about 10 to 1. Their form frequently so far deviates from that of a simple cylinder as to present slight constrictions or undulations. And occasionally they even exhibit a kind of cæcal pouch or blind offset of greater or less length. These pouches usually spring from the lower extremities of the tubes, which generally have a somewhat increased diameter in their neighbourhood.* But with these exceptions, the gastric tubes form simple, straight cylinders, which only widen where they open on the inner surface or cavity of the stomach.†

* These appearances are generally more marked in the separated fragments of a specimen, or on its exposed edges and surfaces, and are certainly often absent. From this and other reasons I have long entertained the suspicion that they are chiefly due to mechanical violence.

† A widening of diameter which obviously cannot exceed the thickness of the matrix around each tube, and may therefore be easily estimated from the amount of this latter tissue seen in looking at any vertical section of the mucous membrane *in situ*.

The *limitary* or *basement membrane* which forms these tubes precisely resembles this delicate homogeneous layer of the mucous structures generally, except perhaps in the fact of its possessing an even greater tenuity. It is usually seen only as a dark outline, bounding some part of a tube that happens to have been isolated entire. Rarely, however, it may be identified as a delicate, floating, and collapsed fold, which, on the addition of a dilute alkali, first swells up, and then altogether disappears. On the ridges which unite the tops of the tubes it is quite impossible to separate it from the subjacent structures;—an intimate adhesion which forms a striking contrast to the ease with which we can often isolate the tubes themselves.

The *contents* of these tubes appear to be everywhere alike. In the upper fourth or fifth of their length, they contain a single layer of columnar epithelium (*c*, *fig.* 246.). Seen as isolated cells, the particles of this epithelium have a cylindrical shape, and enclose a very distinct nucleus near their attached extremity. But when we look at them in their natural situation, from the free side of the mucous membrane, we see that they are rather hexagonal prisms than cylinders; and contain nuclei, which appear to lie so near to their lower ends, as to be separated from the basement membrane by little more than by the cell-wall at this part. The remainder of the tube is occupied — and under normal* circumstances appears to be filled — by oval or somewhat angular cells (*a d*, and *b*, *fig.* 246.) of considerable size. The largest of these oval cells are about $\frac{1}{1200}$th of an inch in diameter. They have a more or less distinct membranous wall. The nucleus they contain is usually in contact with that side of their parietes which is attached to the basement membrane of the tube; and it sometimes exhibits a nucleolus. Their contents are finely granular, with here and there refractile dots that have a close resemblance to oil globules. And the author has been able to establish the fact, that a large proportion of these cells enclose, beside the above granular material, numerous (5—15) pale, flat, and extremely delicate cytoblasts. Whether the centre of the layer formed by these cells constitutes a distinct calibre or cavity of the tube, — or whether it is merely an interval occupied by granules or cytoblasts — he is unable at present to decide.

As has already been hinted, the gastric mucous membrane is distinguished from most other parts of the body, not only by the great delicacy of its structure, but by the complexity of its arrangement; and above all, by the remarkable facility and rapidity with which it undergoes disorganization and de-

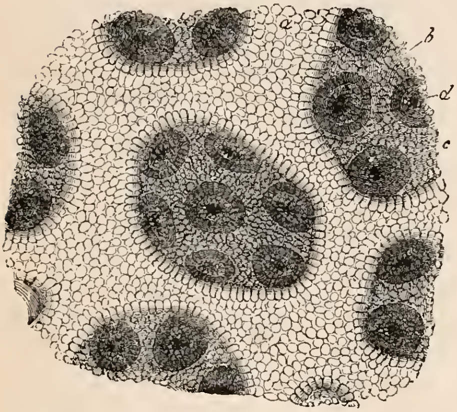
* It is very common to find portions of the tubes quite devoid of these cells, and occupied by a granular substance, with nuclei and cytoblasts in varying proportion. But I believe that this appearance, which is especially frequent in the blind ends of the tubes, is generally the result of mechanical injury of the original cells. (Compare p. 324.)

composition. These changes seem to be the result, partly of putrefaction, partly of a self-digestive process. And since we scarcely ever have any opportunities of examining the perfectly healthy stomach of Man immediately after death, we are compelled to lay unusual stress upon the structure seen in those of the higher Vertebrate animals which approach most nearly to the human conformation of this organ.

Among the various domestic Mammalia most accessible for such purposes, the structure and habits of the Dog render its stomach, in many respects, one of the best we can select for examination.

In this animal, the tubes of the *cardiac* extremity (B, *fig.* 248.) begin on the free or

Fig. 247.



Mucous membrane from the middle of the Dog's stomach, as seen from the free surface. Magnified 150 diameters.

a, ridges which intervene between the primary tubes, covered by columnar epithelium; *b*, primary tubes, lined by similar columnar cells; *c*, secondary tubes, given off from the preceding, and lined, at their commencement, by similar cells; *d*, central calibre, or cavity, of a secondary tube.

cavitary surface of the organ, by apertures which form the intervals of a kind of network of ridges. These apertures are polygonal, or irregularly six-sided, and the tube into which each soon merges has a diameter that is very little less than the distance between the ridges; — on an average about $\frac{1}{200}$th of an inch. The tube now proceeds downwards for a short distance, before bifurcating into two smaller tubes. And each of these again divides at a further stage of its descent. In this manner, what was at first a single large cylinder, ends as a bundle of about four or five small tubes, which are collectively enclosed in a portion of matrix thicker than that occupying their interstices.

At the *pyloric* extremity of the organ, the tubes (A, *fig.* 248.) commence by apertures, which have a diameter twice as great as those seen in the cardiac region, and from hence they pass vertically downwards for some distance, with a simple cylindrical form. All the terminal branches of these long pyloric tubes are for the most part given off at nearly the same height, so that they constitute only one-sixth, or thereabouts, of the whole thickness of the mucous membrane, instead of about five-sixths, as in the cardiac extremity. In both the above regions, however, the number of these terminal tubes is rarely less than three, or more than six. Their diameter is generally about one-third that of the larger and simple tube from which they originate. And the total bulk of the bundle which they form, as seen on transverse section, is as nearly as possible equal to that of the primary tube.

But these differences in the width and ramification of the cardiac and pyloric tubes are accompanied by a much more remarkable and important contrast in the form, size, and arrangement of their respective contents.

The whole of the *pyloric* tube (A, *fig.* 248.) is occupied by a single layer of columnar epithelium, the cylindrical or slightly prismatic cells of which are placed vertically to the basement membrane, and contain a very distinct nucleus near their attached extremity. The only difference offered by these cells in the terminal branches of the tube is, that they are shorter in proportion to their width, and enclose darker and more granular contents.

Fig. 248.

Tubes from the cardiac and pyloric regions of the Dog's stomach, to show the contrast of their structures. Magnified 60 *diameters. Altered from Koelliker.*

A. pyloric tube; *a*, primary tube; *b*, three secondary tubes. B. cardiac tube; *a*, primary tube lined by columnar epithelium; *b*, two secondary tubes; *c*, four terminal branches containing large oval cells.

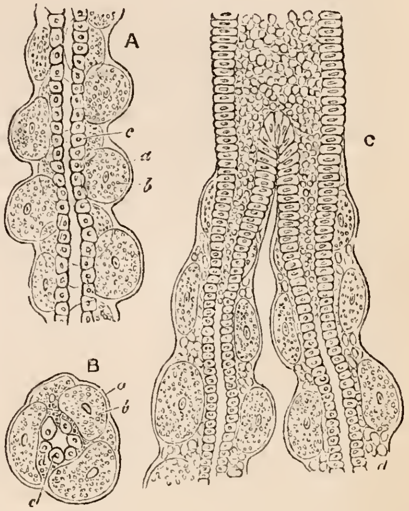
They everywhere bound a tube with a distinct calibre.

In the *cardiac* region, it is only the ridges, and the upper part of the tubes, which are covered by columnar epithelium. At the first (B *b*, *fig.* 248.) or second bifurcation of the primary tube, the character of its lining altogether changes: and from hence onwards to their rounded blind extremities, the secondary tubules are immediately lined by peculiar oval cells (B *c*, *fig.* 248.). These cells are analogous to those seen in the human stomach. They differ however from them, not only in their great size, and more distinct walls, but also in the fact, that they generally bulge the basement membrane of the tube, so as to give it a somewhat moniliform outline. A closer examination shows this appearance to be caused by the prominent cells occupying irregular heights around the wall of the tube.

On getting the middle of such an isolated tube into the focus of the microscope, we find that in the higher part of the tubule, near where it opens into the primary tube, the oval cells, which are always in immediate contact with the basement membrane, form a double row with a somewhat sinuous interval. This interval is a distinct though narrow calibre. Below this visible calibre, I had long been aware that the similar interval between the larger cells was occupied by an immense number of small nucleated cells or cytoblasts,—many of which are firm, with distinct and somewhat angular outlines; while others are excessively delicate, pale, flattened, oval, transparent, and of equal or much smaller size. And the more skilful manipulation of Koelliker has recently enabled him to state, that the centre of the tube presents a continuous narrow calibre or cavity (A, *fig.* 249.), which is immediately bounded by these small, roundish, or angular cells (*c*, A and B). Between these small cells and the limitary membrane, the large oval cells are interposed (*b*, A and B). Below, the latter often seem to form the sole contents of the tube.

The truth of Koelliker's description I can fully substantiate; so far as regards the upper part of these secondary tubes, in the cardiac five-sixths of the organ. Even the blind extremities of the tubes seem to have their axes occupied by the delicate cytoblasts previously alluded to; but they are here, so far as I can see, disposed irregularly. Higher up, the cells are more angular, and possess more distinct outlines; and are often arranged in two rows, which are in contact at the centre of the tube. It is only towards the apertures of the secondary tubes, where the oval cells are beginning to be more thinly scattered prior to their disappearance, that these small cytoblasts appear to form a distinct calibre or tubular cavity of appreciable width. Here they merge into the columnar form;—a change which begins by their becoming elongated towards the axis of the tube, and allowing water to develope a distinct cell-membrane at this part (C, *fig.* 249.). But there are many appearances which render it by no means impossible that the whole length of the tube possesses a narrow calibre, formed by a regular arrange-

Fig. 249.



Portions of tubes from the cardiac extremity of the dog's stomach. Magnified 350 diameters. (Partly after Koelliker.)

A. portion from the middle of such a cardiac tube; *a*, limitary membrane of tube; *b*, large oval gastric cell; *c*, smaller axial cells. B. Same seen in transverse section; *a*, *b*, *c*, as above. External to c are seen indistinctly some delicate cytoblasts; *c*, junction of the primary and secondary tubes, showing the mode in which the small axial cells of the latter are continuous with the columnar cells which form the epithelium of the former.

ment of these small cells. While I have no doubt that the interstices left between the large cells and this central tube of epithelium are also filled up by numbers of cytoblasts, of excessive delicacy, and various degrees of minuteness (*d*, B and C).

Besides these free cytoblasts within the tube, we may find others of endogenous origin. Very careful observation of the large oval cells will show that they enclose cytoblasts in addition to their minutely granular contents (compare *b*, *fig.* 246.). The number of these cytoblasts appears to vary from two to twenty in different cells. They are excessively delicate, of about $\frac{1}{3000}$th inch diameter: their shape is a flattened oval; and they contain a bright spot or nucleus. They seem to be chiefly in contact with the inner surface of the mother-cell; so that in many animals, specimens of their outline can often be distinctly seen through the nearly transparent wall of this cell under the higher powers of the microscope. They may, however, be easily overlooked. And their distinctness never equals that of the proper nucleus of the cell; closely as they resemble this structure in size and shape. They may sometimes be seen projecting from the broken half of a mother-cell; or set free from it, owing to its having been ruptured by the rapid endosmose of water. But they are very quickly dissolved or burst, by contact with most of the fluids which are generally used in preparing such specimens for microscopic examination.

During the five years that I have made the stomach an object of frequent (though interrupted) research, I have examined numerous specimens from the perfectly fresh stomachs of about thirty species of Vertebrata. The following is an outline of the few results I have obtained. As regards the *pyloric* tubes, those of the Cat, Rabbit, Hog, Ox, and Guinea-pig, resemble those of the Dog, in containing a columnar epithelium, and having a distinct calibre to their termination. Those of the Horse resemble the tubes of the human stomach in possessing the oval or gastric cells. In most, if not all of these animals, the tubes ramify. As respects the *cardiac* tubes, the minute central calibre observed by Koelliker in those of the Dog appears to be also present in the Cat and Guinea-pig; and, from analogy, is not unlikely to exist in most Vertebrata. The large oval cells are the rule throughout the Vertebrate kingdom. And in many Reptiles, as well as in the very young animals of most orders, the numerous cytoblasts enclosed by these cells are much more distinct. In only two instances have I found no large cells present in the cardiac tubes, and in both of these, the stomach was evidently disorganized by commencing putrefaction. In some Fishes, however — such as the Mackerel — it is only the middle or apex of the *V*-shaped stomach which is occupied by tubes. And in the Minnow, Carp, and Tench of the Cyprinoid genus, as well as in the river Lamprey (*Petromyzon fluviatile*) no tubes are present. Finally, while there are many species in which the gastric structures appear to be softer and more delicate during the time of digestion than in the fasting state, in none have I been able to verify the least difference in the morphology of the organ at these two periods.

Those who are familiar with the difficulties that oppose the successful examination of the softer tissues of the animal body will probably bear with me if I end this description by what may seem a superfluous caution to the observer. There are many appearances seen in these delicate tubes, which are produced by the mechanical violence necessary to their isolation, aided by the softening of incipient putrefaction or self-digestion, or by the endosmose of the dilute fluids which are sometimes added to such specimens in preparing them for the microscope. Thus the tubes often deviate from the above account in the absence of gastric cells, in the presence of short branches that are given off near their blind extremities, and in the spiral or bulbous shape which these ends sometimes assume. Indeed, when we reflect upon the extreme tenuity of their basement membrane, the nature of their contents, and the firmness with which they are imbedded in a dense areolar and muscular tissue, we shall scarcely be surprised to find, that the violent disruption of these attachments can distort the tubes, or break up their soft contents. But the careful manipulation of perfectly fresh specimens, in a proper fluid medium (such as the serum of the blood, or a strong solution of common salt) renders these appearances so rare, as to render it highly probable that they are accidental. While conversely, the application of a slight pressure, the use of water and dilute acids, and the commencement of digestive or putrefactive softening, will often produce them in a specimen from which they were formerly absent.

In addition to the cylindrical tubes, some * anatomists have found in the stomach ramified glands, which end in *acini* or dilated extremities. These are stated to occupy the neighbourhood of the pylorus, where they form a kind of transitional structure between the gastric and the duodenal glands. I have once or twice seen appearances in the tubes of this part which corresponded pretty closely with the above description. In two other instances, a single flask-shaped dilatation was appended to some of the ordinary tubes, which it thus doubled in diameter. But the arrangement of these latter dilatations, as well as the condition of the remainder of the specimens, left me little doubt that they were due to accidental violence, which had distended the terminal branches of a tube with a large portion of its displaced contents. While their shape and situation (in the mucous membrane itself, instead of its submucous tissue) sufficed to show that they were not lenticular glands; — an argument which will equally militate against the notion of their being a transition to the duodenal glands, since these occupy a similar position.

Lenticular glands are also found in the stomach. As regards their shape, size, situation, and contents, they correspond so completely with the solitary glands of the intestine, that we may refer the reader to these for their special description. Their number varies extremely. Sometimes it is impossible to find any. In other specimens, they are scattered more or less thickly throughout the whole organ. They are said chiefly to affect the lesser curvature; but I have seen them sown very plentifully over the pyloric region only. In children, they are rarely absent. And among the brute Mammalia, they are found occasionally in the Dog †, and constantly in the Pig. ‡ Structures more or less analogous to these glands probably also exist in the Beaver, Kangaroo, Dugong, and many other animals.

Matrix. The cylindrical tubes of the stomach are united to each other, in their whole length, by a sparing quantity of a fibrous

* Bruch (in Henle and Pfeufer's Zeitschrift. f. Rat. Path. Bd. viii. p. 272. *et seq.*); Ecker (*id. op.* 1852. p. 244.). Compare Bischoff (in Mueller's Archiv. 1838. p. 503.)

† Bischoff, *Op. cit.* p. 510.

‡ *Id. op.*; also Wasmann (De Digestione Nonnulla. Berlin. 1839. p. 8.), and Koelliker, *Op. cit.* p. 150.

network or *matrix;* — their blind extremities being also imbedded in a considerable stratum of this texture, which is continuous with that surrounding their sides. The arrangement of the latter part of it is best seen by making horizontal sections of the mucous membrane, so as to cut transversely across the gastric tubes at different heights. Its quantity is small in proportion to the diameter of the tubes. And in it we may recognize, besides cut extremities of vessels, indistinct concentric fibres, which appear to surround the tubes, and decussate with each other. In the ramified tubes of many animals, each original tube, and its set of secondary branches, is enclosed in a tolerably thick sheath of this kind, which gives off slenderer partitions of the same nature between the smallest individual tubes. On the surface of the stomach, this matrix is nearly homogeneous; but its fibrous character is more distinct at the deeper parts of the membrane, and in those tubes which occupy the neighbourhood of the pylorus. Here its quantity is also increased. Many years ago, the author was struck with the remarkable difference between that layer of this fibrous tissue which lies beneath the tubes, and the submucous areolar tissue upon which it is placed; — the former being characterized, not only by its darker colour, and its dense and closely interwoven texture, but also by its being much less acted on by acetic acid. But Middeldorpf* has since made the important discovery, that this peculiar layer, which extends from the cardia to the anus, is in reality composed of a mixture of areolar tissue, and organic or unstriped muscle: — the fibres of the latter structure being arranged in two series of bundles that decussate with each other at an acute angle. Externally, these fibres are conjectured by Koelliker to be more or less continuous with the ends of the oblique fibres of the muscular coat. Internally, Bruecke states them to pass upwards, in small bundles, between the several tubes. This statement is to some extent confirmed by Koelliker, who has seen numerous cells very like the fibre-cells of organic muscle occupying this situation in Man, some Ruminants, and the Pig. In the latter animal, bundles of these fibres penetrate the rudimentary villi of the pylorus, and occupy their axes. Of the function of these muscular-fibre cells we know nothing. But, from their arrangement, it would seem not impossible that they are destined to maintain the tubes in their normal situation, against the disturbances which the contractions of the proper muscular coat might otherwise produce.

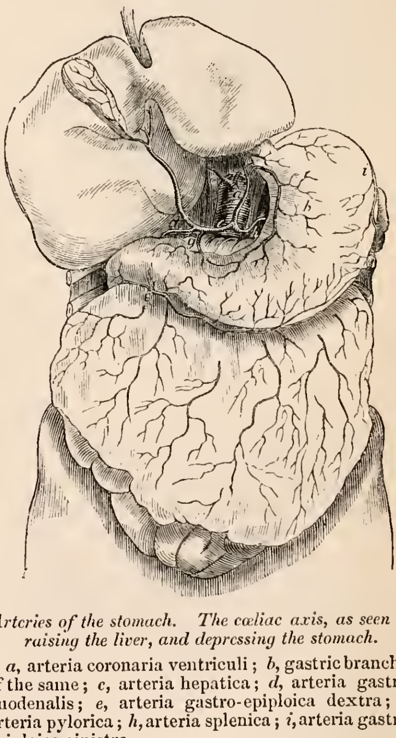
Areolar tissue. A layer of loose *submucous areolar tissue* (the *tunica nervea* of some authors) connects the mucous membrane of the stomach with the proper muscular coat previously described. Seen in vertical section, its thickness is a little greater than that of the denser muscular stratum which receives the extremities of the tubes. Its constituents are the ordinary white and yellow fibrous elements; the elastic filaments of the latter being chiefly of small size. Externally, it is pretty firmly connected with the muscular coat, and appears to receive many of its fibres. But internally, where it approaches the fibrous matrix, its meshes are very large and loose, so as to allow of the mucous membrane being thrown into folds by the contraction of the muscular tunic. It contains the vessels, nerves, and lymphatics destined for the supply of the mucous membrane.

* De glandulis Brunnianis. Vratisl: 1846.

The *vessels* of the stomach are very large and numerous. The arteries are derived from the abdominal aorta. The veins empty themselves into the *vena portæ*, which ramifies in the liver.

The *arteries* of the stomach all come off from the cœliac axis. This vessel, which leaves the aorta opposite the first lumbar vertebra, continues obliquely forwards as a short thick trunk for a distance of about half an inch; when the "axis" ceases, by giving off, at right angles to itself, three large branches: — namely, the *gastric*, *hepatic*, and *splenic*.

Fig. 250.



Arteries of the stomach. The cœliac axis, as seen by raising the liver, and depressing the stomach.

a, arteria coronaria ventriculi; *b*, gastric branches of the same; *c*, arteria hepatica; *d*, arteria gastro-duodenalis; *e*, arteria gastro-epiploica dextra; *g*, arteria pylorica; *h*, arteria splenica; *i*, arteria gastro-epiploica sinistra.

The *arteria coronaria ventriculi* (*a*, *figs*. 250, 251.), or proper *gastric* artery, is the smallest of these three. It passes upwards and towards the left side, beneath the peritoneum which forms the dorsal and outer surface of the sac of the omentum; until, arriving nearly at the upper extremity of this cavity, it turns forwards in a slight projection or fold of the serous membrane. In this fold, it has a very brief and somewhat arched course, which brings it to the left end of the smaller curvature of the stomach. Here it passes between the two layers of the gastro-hepatic omentum. From hence it continues, in a very tortuous course, along this curvature; lying close to the stomach, and diminishing in size by giving off frequent branches; until, towards the right or pyloric extremity of the organ, it is lost by anastomosing with the branches of the hepatic artery.

Its larger or named branches are the *œsophageal* and the *gastric.* The first are given off from the highest point of the vessel, or where it enters the gastro-splenic omentum. They run upwards to the œsophagus, and take a longitudinal course; so as to pass, with this tube, through the opening in the diaphragm. And they anastomose with the thoracic vessels distributed to this tube from the aorta. The *gastric* ramifications (*b, fig.* 250.) run downwards from the coronary artery on both surfaces of the stomach. They inosculate, on the left, with small branches from the splenic artery; towards the middle of the organ, with the gastro-epiploic branches; and at the pylorus, with the superior pyloric artery.

The *arteria hepatica* (*c, figs.* 250, 251.), which is the next largest branch of the cœliac axis, passes for a short distance outwards, and slightly forwards, from the axis or common trunk, to reach the commencement of the duodenum. It now runs almost vertically upwards between the two layers of peritoneum that form the gastro-hepatic omentum, and in front of the foramen of Winslow (though still with a slight inclination towards the right side), to end by being distributed in the liver. In this course, it gives off two branches, — the gastro-duodenal and the pyloric — both of which take an important share in supplying the stomach with arterial blood.

Fig. 251.

Arteries of the stomach. The cœliac axis, as seen by raising the stomach, so as to expose the arterial branches behind it.

a, arteria coronaria ventriculi; *c*, arteria hepatica; *d*, arteria gastro-duodenalis; *e*, arteria gastro-epiploica dextra; *f*, arteria pancreatico-duodenalis; *g*, arteria pylorica; *h*, arteria splenica; *i*, arteria gastro-epiploica sinistra.

The *gastro-duodenalis* (*d, figs.* 250, 251.) is the first and largest artery of these two. It leaves the hepatic vessel behind the duodenum, passing vertically downwards across the intestine to the lower border of its first portion. In this course, it gives off a few small branches to the neighbouring parts of the stomach and intestine; some of which twigs have been distinguished as the *inferior pyloric* arteries. And at the inferior margin of the bowel, the gastro-duodenal artery bifurcates into two: — a large *gastro-epiploic*, and a small *pancreatico-duodenal* branch.

The *gastro-epiploica dextra* (*e, figs.* 250, 251.), the large vessel which continues the *gastro-duodenalis,* is so named from its situation between those layers of the great omentum which descend from the stomach to form the "epiploon" or apron-like fold that covers the greater part of the intestinal canal. Beginning at the lower border of the duodenum, the artery runs from right to left, along the lower margin or great curvature of the stomach, and at a little distance from it, with what is usually a wavy or tortuous direction. In this course, it gives off branches which pass upwards on both surfaces of the organ; as well as others of less importance, both upwards and downwards, to the fatty and serous tissues of the omentum itself. And rather beyond the middle of the stomach, or towards its cardiac pouch, it ends by uniting with a corresponding branch, of smaller size, from the splenic artery.

The *pancreatico-duodenalis* branch (*f, fig.* 251.) has precisely the situation and distribution which its name would imply. It runs between the duodenum and the head of the pancreas, lying in the concavity formed by the horse-shoe curve of the canal, or around the convexity by which the gland fits into this hollow. It gives off ramifications to both these structures, and ends by anastomosing with a branch, which comes upwards from the superior mesenteric artery and also occupies the same interval between the pancreas and the lower portion of the duodenum.

The *arteria pylorica* (*g, figs.* 250, 251.), which is sometimes distinguished by the title of the *pylorica superior* from the smaller branches of the gastro-duodenal above alluded to, is generally given off from the trunk of the hepatic artery opposite to the upper border of the duodenum. More rarely it is derived from the commencement of its gastro-duodenal branch. In either case, it enters between the layers of the gastro-hepatic omentum, and runs in this fold, from right to left, along the upper margin or lesser curvature of the stomach, to join the coronary artery from the cardiac extremity of the organ. It gives off numerous branches to both surfaces of the organ.

The *arteria splenica* (*h, figs.* 250, 251.), or second branch of the cœliac axis, has no direct connection with the alimentary canal, until near its division into the terminal trunks by which it enters the spleen. Here it gives off a left *gastro-epiploic* artery; and numerous small and short vessels, the *vasa brevia.*

The *gastro-epiploica sinistra* (*i, figs.* 250,251.) leaves the trunk of the splenic artery close to where this divides at the inner surface of the spleen. It passes downwards, forwards, and towards the right side, first lying for a short distance in the gastro-splenic omentum, and then entering between the layers of the great omentum which is continuous with this fold. It then runs along the lower border or great curvature of the stomach, to anastomose with the corresponding vessel on the right side. Like it, it supplies branches to both surfaces of the stomach.

The *vasa brevia* are numerous small branches which come from the primary and secondary divisions of the splenic artery, and run in the gastro-splenic omentum to the cardiac pouch. Here they break up and anastomose with each other, as well as with the coronary and left gastro-epiploic arteries.

The *veins* of the stomach are the *superior pyloric*, and the *right* and *left gastro-epiploic.*

The *vena pylorica superior* receives and continues a large vein, which corresponds to the coronary artery, and takes a similar (but reversed) course along the lesser curvature of the stomach to the pylorus. It now passes upwards for a little distance, before opening into the *vena portæ* (*a, fig.* 281.) near its termination in the liver. In other instances, it bends down to join the splenic vein.

The *vena gastro-epiploica dextra* corresponds to its artery in the greater part of its distribution. It usually ends by emptying itself into the superior mesenteric vein, just before this forms the *vena portæ* by joining with the splenic vein (*e, fig.* 281.).

The *vena gastro-epiploica sinistra* also runs with its artery, and joins either the splenic vein, or one of its primary branches.

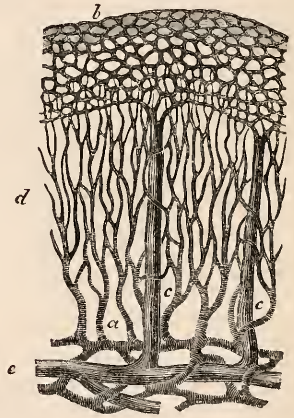
All of the foregoing vessels are characterized by the great freedom and frequency of their inosculations in every stage of their course from the aortic to the portal trunks. This condition is especially well marked in the arteries. And, as ordinarily injected, the latter appear to be both larger and more numerous than the arteries distributed to an equal bulk of most of the other structures of the body.*

Their tortuous course, and their loose connection with the stomach, chiefly refer to the distention of this organ. For as the stomach expands between the laminæ of peritoneum, it gradually straightens these vessels, and alters their position with respect to itself and to each other.

The distal branches of the arterial and venous trunks perforate the muscular coat at different intervals, by twigs which unite with each other in the loose submucous areolar tissue, so as to form two broad and somewhat flattened networks: — one, which is composed of small arteries, and another, of veins. The vessels of the latter plexus are, as usual, both larger and more numerous than the corresponding arteries.

Capillaries. — The arterial branches which leave the above sub-mucous network, to enter the dense muscular layer of the matrix of the stomach, divide here once or twice. And their ultimate ramifications, which have a diameter of about $\frac{1}{1500}$th to $\frac{1}{1800}$th of an inch, pass vertically upwards, along the sides of the tubes to their upper apertures, where they form a superficial network of capillaries. In passing

Fig. 252.



Plan of the vessels of the mucous membrane of the stomach, as they would be seen in a vertical section.

a, arteries from the plexus occupying the submucous areolar tissue; *b*, superficial plexus of capillaries occupying the ridges of the mucous membrane; *c*, veins passing downwards between the gastric tubes; *d*, capillaries between and around the tubes; *e*, plexus of arteries and veins occupying the submucous areolar tissue.

upwards, they also give off other capillaries; which surround the tubes, at all parts of their height, with a second and deeper network. The meshes of this latter plexus are somewhat oblong, but less decidedly so than those of the capillary network of striped muscle; and are about $\frac{1}{100}$th to $\frac{1}{250}$th of an inch in size. The capillaries which compose them are, on an average, little more than $\frac{1}{5000}$th of an inch in diameter. The more superficial network is contrasted with this deeper one, not only in the fact that its capillaries are about double the above diameter (or

* Assuming this fact to be as true as it seems to be, it becomes interesting to inquire what peculiarities of the circulation may be presumed to be connected with it. Other things being equal, the passage of a larger quantity of blood to and from an organ may be fairly supposed to be associated with a greater amount of that change which absorption or secretion there impress upon this fluid. Again, Volkmann's researches have shown that the anastomosis of channels diminishes the resistance in their interior; — a diminution which, if not met by any counteracting circumstance, would increase the velocity of their contents. But the most plausible conjecture that can at present be offered is, that this increase in the number of these small arteries, — which have a distinctly muscular structure, and are plentifully supplied with nerves, — has reference to that efficient and sudden control of their calibre which the varying exigencies of their capillary circulation would seem to imply.

$\frac{1}{2500}$th of an inch), but also in its meshes being nearly twice as close (or about $\frac{1}{300}$th to $\frac{1}{600}$th of an inch). But the two plexuses inosculate so freely, as to be quite continuous with each other at the upper apertures of the tubes. As

Fig. 253.

Superficial capillaries of the mucous membrane of the human stomach, from an injected specimen. Magnified 70 *diameters.*

a, ridges intervening between the stomach-tubes; *b*, capillaries occupying the ridges; *c*, orifice of a stomach-tube.

regards the form of the superficial network, it may be stated to correspond exactly with the intervals of the primary tubes. For the ridges which occupy the surface of the organ are all, as it were, moulded upon capillaries, the union of which forms what we may distinguish as a primary network, that surrounds the aperture of each tube with a capillary loop. In Man,* however, this comparatively simple network is complicated by the addition of other meshes, which lie on either side of it, and just within the orifices of the tubes. In their shape and size, these closely resemble the loops beneath the ridges, and are, indeed, no way distinguishable from them except in their situation. Below, their diameter diminishes, their loops elongate, and they finally merge into the general network which surrounds the tubes.

It is from the large capillaries which compose the superficial network that the radicles of the veins almost exclusively arise. They begin as small vessels of about $\frac{1}{1500}$th of an inch in diameter; and by one or two successive unions of these and their resulting larger branches, they soon attain a width of about $\frac{1}{400}$th of an inch. They now pass vertically down the intervals between the tubes, to open into the flattened venous plexus which occupies the submucous areolar tissue.

The general result of this arrangement on the circulation in the stomach seems to be, that the blood which has already traversed the capillaries of its tubes is passed on to its surface. Hence in respect to their situation and size, these superficial capillaries of the gastric mucous membrane offer a distant resemblance to veins. This fact, as well as their connection, both with small arteries on the one hand, and with confluent capillaries on the other, renders it probable that the velocity of their contents exceeds that of the blood which circulates in the capillaries of many other tissues. Such a peculiarity would admirably adapt them to that absorptive office which their mere situation on the cavitary surface of the organ indicates as one of their chief functions.

Changes in the stomach during digestion.—The introduction of food into the healthy fasting stomach gives rise to two chief alterations in the organ. Its muscular coat is excited* to movement. And, at the same time, its mucous membrane deepens from a pale to a bright pink colour†; and begins to pour forth a liquid secretion—the *gastric juice.*

Gastric juice.—An inquiry into the characters of the gastric juice is opposed by many difficulties. For it is obvious that the properties of this or any other secretion can only be established from its examination in a state of perfect purity. While the situation and functions of the stomach are such that, under natural circumstances, its secretion is necessarily mixed with many other substances. It is true that the bile often found ‡ in the stomach during fasting is shut out from its cavity, during digestion, by the closure of the pylorus. But, on the other hand, the saliva, which generally covers the mucous surface of the empty organ, as a thin viscid layer with a superficial alkaline reaction, is swallowed at this period in much larger quantities; while the food itself forms an equally constant impurity. To such less avoidable sources of error are often added the alterations produced by disease in the unhealthy individual, or by putrefaction or digestion in the healthy subject after death. And though even the most careful study of all these circumstances will scarcely explain the discrepancies and contradictions of numerous (and apparently faithful) observers in their accounts of the gastric juice,—still they evidently constitute conditions which, according as they are obviated, or noticed, or neglected, will respectively render any particular observations valid, or comparable, or utterly useless. §

* In many animals the superficial network appears limited to this simpler form; especially in the cardiac region, where the intervals of the tubes are smaller.

* See *ante*, p. 312.

† Beaumont, *Op. cit.* pp. 94. *et seq.*

‡ See *ante*, p. 315.

§ The above remarks form a key to the following historical summary of the more important observations which have been made on this fluid; as well as a reason why the author has reduced it to a mere enumeration,—such as will not, however, preclude a fuller subsequent reference, where this is required.

Reaumur, in the year 1752, obtained an artificial digestive fluid from the stomachs of animals by means of sponges attached to strings (Mém. de l'Académie, 1752. pp. 705. *et seq.*). About 1780, Spallanzani (Ueber das Verdauungsgeschaeft. Leipzig, 1785) adopted the same method; and also examined matters which had been vomited. He thus determined the gastric juice to be a neutral, antiseptic solvent. He quotes Scopoli and Gosse to the same effect. Carminati (Untersuchungen ueber die Natur des Magensaftes, 1785) also deduced his results from substances vomited; and found that it was only the acid fluid secreted after eating which possessed antiseptic and digestive powers. Several observers, however, — among whom were Viridet

Physical Properties.—Pure gastric juice is a structureless, limpid, and transparent fluid, of a pale straw colour. Its taste is slightly saline, and distinctly acid. And it has a peculiar faint odour, which is probably characteristic for each of the different* species of animals, like the smell of the blood from whence it is no doubt derived.

Where, as is often the case, the gastric juice is mixed with saliva, mucus, or relics of the food, its appearances will of course differ from those above described. The froth of the saliva sometimes distinguishes this admixture. The mucus thus added is ropy or viscid, and generally presents scaly epithelium, which, together with its neutral or alkaline character, betray its origin from the mouth or œsophagus. Both it and the fragments of food are frequently deposited from the gastric juice, as a dirty flocculent sediment. And they may always be removed from it by careful filtration ; when the fluid loses its greyish, brownish, or turbid character.

The *specific gravity* of the gastric juice was observed by Silliman to be about 1005·0. But from the condition of the specimen he examined, and the mode of weighing† he adopted, very little reliance can be placed on this statement. Lassaigne ‡ also made direct observations with the same view, and found that the irritated empty stomach poured forth a fluid of sp. gr. 1001·0 ; while that secreted on the contact of flesh was 1005·0, and with bread 1010·0. But it must obviously be very difficult directly to determine the specific gravity of such a fluid, in the small quantities in which it is generally obtained. The per-centage of solid contents is more easily estimated.—Tiedemann and Gmelin rated it at 1·95 in the gastric juice of a dog who had been made to swallow small pieces of limestone ; and at 1·6 in that of a horse. Berzelius gives it at 1·27 in the specimen sent him by Beaumont ; Lassaigne at 1·32, and Blondlot at 1·0, from the gastric fistulæ of dogs ; Frerichs (appa-

(De Primâ Coctione, Geneva, 1692), Brugnatelli (Crell's Annalen, 1787), and John Hunter (Animal Œconomy, 2nd ed. p. 205. 1792)—had found that the stomach contained an acid. Macquart (Mémoires de la Soc. Roy. de Médecine, 1786) stated this acid to be phosphoric in the paunch of Ruminants. Treviranus extracted the proventriculus of Birds with water : he thus, amongst other results, was able to confirm Hunter's conjecture, and regard it as lactic acid (Biologie, vol. iv. p. 358. 1814). Chevreul (Magendie's Physiologie, 1st & 2nd ed. 1825, vol. ii. pp. 11, 12.) analyzed a fluid obtained by voluntary vomiting. He not only confirmed the presence of lactic acid, but announced the presence of the muriates of ammonia, potash, and soda; together with an animal substance soluble in water, but not in alcohol.

In 1824, Prout led the way to a better knowledge of this fluid by an analysis of the contents of the stomach in Rabbits during digestion, in which he found hydrochloric acid and chlorides (Philosophical Transactions, 1824, pt. i. p. 45.). Dr. Children confirmed this statement from the gastric fluid of a dyspeptic patient (Annals of Philosophy, 1824, vol. viii. p. 68.). Leuret and Lassaigne, however, using this latter method, confirmed Chevreul as to the presence of lactic acid (Récherches physiologiques et chemiques pour servir à l'Histoire de la Digestion. Paris, 1825.) Tiedemann and Gmelin excited the secretion of gastric juice by introducing stones into the stomachs of animals, and found hydrochloric acid on examining the contents of the stomach after death (Die Verdauung nach Versuchen. Leipzig, 1831). In 1833-4, Beaumont's unique case afforded specimens for three analyses ; by Dunglison, Silliman (Beaumont, *Op. cit.* pp. 69. et seq.), and Berzelius (Annuaire des Sciences chemiques, p. 282.). They all essentially corroborated Prout (Annales de Chemie, t. lix. p. 348.) ; as did Braconnot in 1835, with gastric juice from the sponged stomach of animals. Wasmann, in 1839, made some excellent experiments on artificial digestion with an infusion of pig's stomach ; but added little or nothing to our knowledge of the gastric acid (Nonnulla de Digestione. Berolini, 1839). Huenefeld, adopting Prout's method, obtained lactic acid (Chemismus in der Thierischen Organization. Leipzig, 1840) ; a result in which, as well as in the cause of Prout's and Dunglison's view, Lehmann either preceded or confirmed him (Physiologische Chemie, 1840. Bd. i. p. 284.). Enderlin, however, who examined the digesting stomach of a beheaded criminal, and repeated Dunglison's process, reasserted its results (Liebig's Annalen der Chemie und Pharmacie, 1843. Bd. xlvi., p. 122.) In this year, Blondlot imitated Beaumont's case, by instituting fistulæ in the stomachs of dogs ; and announced biphosphate of lime as the acid principle (Traité Analytique de la Digestion. Paris, 1843). Lassaigne (Journal de Chemie, 1844, pp. 73. 183.) ; and Bernard and Barreswil (Comptes Rendus, 1844, t. xix. p.1285.) made use of the same method ; but denied the accuracy of Blondlot's chemical results in detail, and affirmed the presence of lactic acid. Pelouze corroborated some of their statements (Comptes Rendus, t. xix. p. 1227.) ; as subsequently did Thomson also (Philosophical Magazine, 1845, p. 419.). Schmidt next asserted that the active principle of the gastric juice was hydrochloric acid, modified by combination with the digestive principle ; but did not detail the analyses on which this view was based (Annalen der Chemie u. Pharmacie, 1847, Bd. lxi. p. 311.). Lehmann, in 1849, corroborated the lactic acid view, by examinations of gastric juice from fistulæ (Berichte der Gesell. der Wiss. zu Leipzig. Bd. i. pp. 100. et seq. ; and *Op. cit.* Bd. i. s. 97.). And Frerichs about this time came to the same conclusion (Wagner's Handwoerterbuch der Physiologie, vol. iii. p. 815.) from similar experiments.

But this comparative unanimity in favour of lactic acid was not destined to last long. In 1851, Huebbenet for the first time found a simple method of preventing that admixture of saliva which had hitherto rendered the gastric juice obtained in such experiments with fistulæ an impure secretion. This he did by obliterating the ducts of the larger salivary glands. And the researches which Bidder and Schmidt instituted upon the gastric juice thus procured seem at length to have established, that it is the hydrochloric which constitutes the proper acid of the gastric juice.

[In preparing the greater part of this essay for the press, the author found it impossible to procure a copy of Bidder and Schmidt's valuable Essay ; and was hence only acquainted with such portions of it as are mentioned in Lehmann's (Physiologische Chemie, vol. iii.) recent work ; in the reports given of Huebbenet's Dissertation by Scherer and Valentin, in Canstatt's Jahresbericht (1852, Bd. i.) ; and by Funke in Schmidt's Jahrbuecher (1851, p. 275.).]

* At any rate the author's observations tend to show that this is the case in Man and many animals. Human gastric juice is stated by Dunglison (Physiology, vol. i. p. 503.) to smell of hydrochloric acid. And Beaumont (p. 76.) asserts, that it tastes like this acid in a state of dilution.

† Beaumont, *Op. cit.* p. 72.

‡ *Loc. cit.* pp. 183. et seq.

rently from dead animals) at 1·72, 1·80, 1·15, after feeding with hay, bones, and peppercorns respectively; Lehmann at an average of 1·4; Bidder and Schmidt at 2·694 in the gastric juice of a dog with deligated salivary ducts, 2·883 in another dog in whom they were free, and 1·385 from a sheep. These latter high numbers indicate that, whatever may be the influence of an admixture of food or saliva in increasing the residuum of the gastric juice, it is more than counterbalanced by the loss which attends the analysis of small quantities. The first of these three quantitative analyses by Bidder and Schmidt I have made the basis of a calculation *, according to which the specific gravity of the gastric juice would be 1003·3,—an estimate that tolerably agrees with the observations of Lassaigne and Silliman.

The *quantity* of the gastric juice is even less accurately established. From Beaumont's experiments, it would appear that at least eight ounces may be secreted in an hour. It is, however, not impossible that ten times this amount may be poured out during the digestive process. For Bidder and Schmidt's observations on animals give an average of about $\frac{1}{200}$th of the weight of the whole body per hour, with a maximum of $\frac{1}{20}$th in the same period. But it is probable that the latter proportion exceeds that which could be secreted by a human being † in the same space of time.

Chemical composition.—In inquiring into the chemical composition of the gastric juice, it will be convenient successively to consider its acid, its saline, and its animal constituents.

The gastric acid.—Although this obvious and unmistakeable character of the gastric juice has been recognised for more than 150 years, yet the nature of the acid on which it depends is probably still regarded as uncertain. An impartial and searching criticism of all the numerous and conflicting analyses that have been made would far exceed the limits of this essay:—even had the author (what he has not) the abilities and leisure necessary to such a task. The reader will therefore only expect such a sketch, as may include some of the chief facts which justify us in preferring, if not in adopting, one particular view.

Not to mention those exceptional instances in which acetic, butyric, or other acids, have been found in inefficient quantity in the contents of the stomach, there are at least three views of sufficient importance to demand some notice. The first of these regards the gastric acid as the hydrochloric: the second as the lactic. While the third attributes the acidulous character of the secretion to the presence of a salt, the acid phosphate—or, as it is sometimes incorrectly termed, the superphosphate*—of lime.

The latter view, which denies the presence of a free acid, is the more recent of the three. It rests solely upon the statements of Blondlot †; from whose writings we select some important details, which are directly contradicted by the concurrent testimony of other chemists, and even by his own later researches. According to him, the gastric juice is precipitated by lime, does not act upon chalk, and contains no chloride of calcium. He also states (or rather implies) that biphosphate of lime is decomposed by incineration, so as to leave a neutral residue. Each of these statements is met by Lassaigne, Huenefeld, Melsens, Dumas, Bernard, and various other authorities, with a direct denial. And in a more recent Memoir, Blondlot himself lays especial stress upon the presence of a large quantity of chloride of calcium, the absence of which salt he had previously insisted on.‡ After these remarks, it is unnecessary to detain the reader by any further consideration of the various other errors—qualitative as well as quantitative—which invalidate the chemistry of this observer. But it is impossible to make these necessary allusions to Blondlot's analyses without passing a tribute to his talent, in devising an operation to which we owe all the brilliant experiments that have lately done so much for the physiology of digestion.

Of the two remaining views, the partisans of each were, until lately, so equal in number, in repute, and in the validity of their arguments, that few physiologists could decide in favour of either: and those who could not suspend their judgment; were probably beginning to believe in both.

On the side of lactic acid was the united testimony of Chevreul, Lassaigne, Thomson, Lehmann, Payen, Bernard, and Frerichs; who had all verified its presence in gastric juice, sometimes when unmixed with food. While against the analyses of Prout §, Dunglison, Braconnot, Tiedemann, and others—in which hydrochloric acid was either lost from the

* This calculation is founded on a method suggested by Schmidt, and quoted by Lehmann (*Op. cit.* Bd. iii. pp. 4, 5, 6.). I have assumed that the condensation of the ferment on solution equals that of albumen; that the chlorides of calcium and ammonium stand about midway between those of potassium and sodium in this respect; and that the hydrochloric acid occupies no bulk at all. On these suppositions, the 26·938 grains of residuum would take the space of 23·617 grains of water; whence 1000 — 23·617 + 26·938 = 1003·3.

† In a person of average weight, the above proportion of $\frac{1}{20}$th of the whole body would correspond to a secretion of about seven pints (nearly one gallon) of gastric juice in an hour.

* The formula of which is $CaO, 2\,HO, P^2\,O^5$.

† *Loc. cit.*

‡ Compare *Op. cit.* pp. 246. 250., and Comptes Rendus, t. xxxiii. p. 118.

§ This allusion to Dr. Prout's analyses may seem to require some explanation; the more so, that they have sometimes been misquoted. He analyzed the gastric juice of rabbits who had been fed shortly before death. The contents of the stomach were filtered, and divided into four parts. The first was evaporated to dryness, and ignited. The second was supersaturated with potash, and similarly treated. The third was exactly saturated with the same alkali of known strength. In the case of the first two portions, the saline ash remaining after ignition was dissolved in water, and tested with nitrate of silver for hydrochloric acid. It was presumed that the first method would give the amount of fixed chlorides present; the second, the total amount of residuum, or found in the distilment, of the gastric juice — they* brought forward the fact, that towards the close of the process of distillation, the fixed lactic acid was capable of displacing the volatile hydrochloric from the salts in which it had been formerly combined; leaving lactates and lactic acid, in a thick acidulous residue of a syrupy consistence. They added, that this late appearance in distillation (as shown by nitrate of silver and peroxide of manganese) proves the absence of the free acid; as does also the precipitate effected in gastric juice by oxalic acid, — a precipitate which would not occur in water containing but $\frac{1}{500}$th of hydrochloric acid.

To this one might have answered, that such a displacement of hydrochloric acid could scarcely have occurred in any of these analyses. Dr. Prout examined in vain for organic acids. And just as he expressly affirms, so others imply, their absence. While Dunglison † and Berzelius found that the residuum contained a large quantity of chlorides. And if it be difficult to suppose the chlorides of the gastric juice sufficient, both for a large distilment of acid, and a still larger residuum of salts, — it is even more difficult to imagine (with Lehmann ‡), that the chloride of calcium alone can yield the former, and yet also appear in the latter.

The absence of the ordinary reactions of hydrochloric acid is, indeed, explained by a theory of Schmidt's, which will be noticed again hereafter, and according to which the acid is in some degree fixed and retained by its chemical combination with the organic principle of the gastric juice. He shows that, if a solution of nitrate of silver be added to this secretion, it throws down a precipitate, which consists of chloride and organic matters; while conversely, it leaves some silver in the clear supernatant fluid. But such a fact scarcely requires the aid of the above theory. The way in which the affinity of even small quantities of organic substances can disturb various chemical processes, offers a well-known analogy to this retarded precipitation. And without some such an action really obtained, the non-precipitation of dissolved albumen by gastric juice would (as Blondlot indeed assumes) disprove the presence of both lactic and hydrochloric acids in this fluid.

The analysis of Enderlin, however, carried the investigation a step further, by distinctly asserting the presence of hydrochloric acid in the residuum of the distillation.* And Bidder and Schmidt's recent experiments seem quite conclusive, both as to the presence of this, and the absence of lactic, acid.† These observers avoid distillation, and treat the fresh gastric juice, previously acidulated by nitric acid, with nitrate of silver; so that the precipitate is free from all organic matters. To the supernatant liquid, they add hydrochloric acid, so as to remove all excess of silver; and then determine its bases by evaporation and ignition. These they find insufficient to neutralize the chlorine of the precipitated chloride. And on saturating a quantity of the same juice with potash, baryta, or lime, they find that the amount required for its neutralization is exactly equivalent to the deficiency observed in the previous analysis.

But this leaves us with two gastric acids, the hydrochloric and the lactic. Hence three questions suggest themselves. — (1.) Are they present together? (2.) Do they substitute or replace each other? Or (3.) is the lactic acid a mere secondary and accidental product?

Even since Bidder and Schmidt's analyses, Lehmann has again answered the first of these questions in the affirmative; having found both acids together in a quantity of gastric juice collected from 14 dogs. The second and third questions cannot at present be replied to. As regards the second, we have no valid proof that the species of the animals examined, their health, or even the nature of their food, ever effects any such qualitative alteration in this secretion. In respect to the third, we may point out, that the variable (and often large) quantity of lactic ‡ acid is precisely what might be expected, supposing it to be a secondary production. And, according to Lehmann, the particular variety of lactic acid seen in the stomach is that produced by the fermentation of sugar, and not that obtained from the fluid of muscle. This fact has induced me to conjecture, that the lactic acid thus observed can scarcely be directly secreted from the blood. But it must remain for future experiments to decide, whether its absence in the later (and apparently exact) analyses of Bidder and Schmidt, was due to the exclusion of saliva, to the fresh state in which the gastric juice was examined, to its careful separation from all food and peptone, or, finally, to the avoidance of the process of distillation. Still, waiting

hydrochloric acid, as well free as combined. The third method would allow of the estimate of the free acid. And this, together, with the fixed hydrochlorates of the first method, subtracted from the total of the second, would leave the quantity combined with the volatile alkali ammonia. He thus found, that rather more than half the chlorine present was combined with hydrogen, in the form of free hydrochloric acid, while, of the remainder, nearly half was united with ammonia, the rest with potassium and sodium. A fourth portion was examined in vain for an organic acid. And other salts, such as sulphates and phosphates, were only found in very small quantity.

* Aided and confirmed by the observations of Blondlot (*Loc. cit.*), Huenefeld (Chemismus in der Thierischen Organization, Leipzig, 1840, p. 207. *et seq.*), and others.

† With the "astonishing quantity" of chloride of silver obtained from the distilled liquid by Dunglison, there ought to have been at least half as much lactic acid in the (apparently uninjured) residuum.

‡ Compare *Op. cit.* vol. i. p. 98. and vol. ii. p. 43.

* Lehmann (vol. i. p. 97.) urges against this observer, that, in a previous analysis, he had failed to find carbonate of soda in the ash of the blood: — an argument which seems somewhat invidious as well as inconclusive.

† Lehmann, *Op. cit.* vol. iii. p. 331.

‡ Compare Lehmann, vol. ii. p. 42.; vol. iii. p. 33.

the results of such a laborious inquiry, there seems little doubt that we ought to regard the balance of evidence as inclining decisively towards a single gastric acid, and that acid the hydrochloric. *

Whatever the number or nature of the substances to which this acid reaction of the gastric juice is due, there can be no doubt as to their source: — namely, the blood. And it is to a derivation of acid from some of the constituents of the latter fluid that we must refer the important fact established by Dr. Bence Jones:— namely, that, during digestion, the healthy urinary secretion loses that acidity which is proper to it at other periods.

Salts. — As regards the salts of the gastric juice, we can only refer to the accurate analyses alluded to above; — which, while they confirm the large quantity of chlorides mentioned by most observers, exhibit rather less of the chloride of ammonium than the united (but rather vague) statements of many observers would have led us to expect.

The details of an analysis of the gastric juice may be best comprehended (if not explained) by placing them side by side, with a similar quantitative examination of the *liquor sanguinis.* The following table† exhibits such a comparison, for a thousand parts of both fluids.

	Liquor Sanguinis.	Gastric Juice.
Water - - -	903·	973·2
Animal matters -	88·5	17·0
Mineral substances -	8·6	9·8
Chlorine - - -	3·6	5·6
Sodium - - -	3·3	1·2
Potassium (in dog, ·2?)	·3	·6
Phosphoric acid -	·2	·6
Phosphate of lime -	·3	1·2
Phosphate of magnesia	·2	·2
(Lime corresponding to ·624 Ca. Cl.) -		·3
	1000·0	1000·0

Hence, while most of the blood-salts are present in increased quantity in the gastric juice, the chloride of sodium is so greatly diminished, as to lower the total saline contents of this secretion below those of the liquor sanguinis. While the amount of its hydrochloric acid is so great, as not only to compensate this loss, but even to raise the total of its mineral constituents above that of the liquor sanguinis than before. The origin of this acid is obvious. Its mere quantity is sufficient to refer it to the chloride of sodium, which is the most plentiful chloride of the parent fluid. And the remarkable diminution in the sodium of the secreted fluid further confirms this view. Indeed, it is difficult to avoid noticing, that many of the differences between the salts of the two fluids might be included in some such hypothesis as the following: — (1.) a rapid transudation of the blood-salts generally, followed by their concentration through absorption of part of their water of solution; (2.) a decomposition of about half of the chlorides, probably of the chloride of sodium*; (3.) a return of the base of this salt into the blood.

Organic substance, or Pepsine. — The addition of alcohol to pure gastric juice, or to a watery infusion of stomach, causes a white flocculent precipitate; which, when dried at a low temperature, forms a much less voluminous mass, of a yellowish grey colour, and a somewhat gummy appearance. This substance reddens litmus, and is soluble in cold water; but may be again precipitated from its aqueous solution by alcohol. Its ultimate analysis yields sulphur and nitrogen, together with carbon, hydrogen, and oxygen. But we neither know the exact proportions in which all these elements are present, nor the manner in which they are combined: — and may even doubt, whether its composition is really quite definite and constant in different specimens.

Two analyses of this precipitate have however been made:—one by A. Vogel †, of the extract of Pig's stomach; and one by Bidder and Schmidt‡ of the pepsine obtained from pure gastric juice. They are as follows: —

	Pepsine.	
	Vogel.	Schmidt.
Carbon - - -	57·72	53·0
Hydrogen - -	5·57	6·7
Nitrogen - -	21·09	17·8
Oxygen (+ other elements, and loss)	16·06	22·5

Of these two analyses, the latter is probably the more correct one. It offers us a composition closely resembling that of the various protein compounds, from which it

* It is only many months after writing the above lines that Bidder and Schmidt's admirable treatise (Die Verdauungssaefte und der Stoffwechsel) has come into my hands. From it I may translate the following paragraph (p. 44): "The result of eighteen corresponding analyses was, that pure gastric juice of carnivora, after eighteen to twenty hours' fasting, contained *free hydrochloric acid only*, without a trace of lactic or any other organic acid: while the gastric juice of herbivora contains, with free hydrochloric acid, small quantities of lactic acid; which may, however, be referred to their more amylaceous food."

† Here I have calculated the composition of the gastric juice from the purer fluid of Schmidt's first dog. That of the liquor sanguinis, which is quoted from Lehmann (vol. ii. p. 153.), may be safely (*Id.* p. 179.) extended to this animal. To facilitate comparison, both are simplified to one place of decimals. And for the same reason, the phosphate of lime in Schmidt's analysis has been assumed to be the biphosphate, and divided into phosphoric acid, and neutral phosphate.

* Such a decomposition would obviously present many analogies to an electrolysis. But, at present, we should hardly be justified in naming it after this process. That the acid and base are unloosed and separated is certain. But I think no one who has carefully studied the phenomena of current affinity would like definitely to refer the above decomposition to this cause in the existing state of our knowledge. We may, however, notice, that both the quantity and quality of the chloride of sodium would render it more susceptible to electrolytic action than any other of the salts present in the liquor sanguinis.

† Simon's Beitraege, Berlin, 1843, p. 168.; Ann. der Pharmacie, 1839, Apr. p. 36.

‡ *Op. cit.* p. 46.

differs chiefly in containing about 2 per cent. more nitrogen.

The addition of a few drops of dilute muriatic acid to a solution of this precipitate in cold water, constitutes a liquid which possesses energetic solvent powers over ordinary animal food. Hence the organic substance itself has been termed *pepsine* (πέψσις, *concoctio*) :—a name to which there can be no objection, so long as its meaning is confined within proper limits; and is not extended to imply a single and definite organic compound, capable of digesting all the alimentary principles.*

The chemical properties of pepsine offer a striking resemblance to those of many albuminous compounds. Its chief differences from these substances seem to consist in the fact, that it is little or not at all precipitated from its watery solution, by some of the salts which would throw down dissolved albumen. But the precise degree of this resemblance has been found to vary greatly in different observations. Nor is this want of uniformity surpizing. For, as Frerichs has pointed out †, the various watery extracts of stomach made use of in such experiments have all been mixtures of gastric juice with a variable quantity of albuminous matters, from which substances the pepsine is but partially set free by the subsequent process of purification. To this fact we may add, that it is not impossible the quantity and quality of the mineral constituents contained in these impurities have also affected the results. Frerichs therefore examined a quantity of the gastric secretion, which had been obtained from fistulæ; and from dogs who had been made to swallow indigestible substances, such as pebbles and peppercorns. In such cases saliva would probably form the only impurity.

The reactions of gastric juice, and probably of pure pepsine, are as follows: it is not precipitated by boiling, by ferro-cyanide of potassium, sulphate of copper, alum, chloride of iron, or mineral acids. It is precipitated, though not completely, by bi-chloride of mercury. Carbonates of the alkalies give a precipitate of its lime salts. And the soluble salts of silver and lead throw down the chlorides of these metals. In all of these instances a portion of the pepsine is carried down with the precipitate. In the case of the lead, the greater part of the pepsine is thus deposited; but almost all of it may be recovered by washing.

Action of the gastric juice. — It is to the repeated and careful experiments on artificial digestion, which were begun by Eberle, and continued by the various observers before alluded to*, that our knowledge of the details of stomach-digestion is chiefly due. This method of inquiry has not only allowed a continuous and close inspection of changes which must have escaped observation in the living body, but has so varied the several conditions of the solvent process, as almost to acquaint us with the share which each takes in the final and united result. In short, these "questionings of nature" have so far been answered, that we may be said to know, not only what substances the stomach digests, but by what means it digests them. Of the nature of this process, however, we are still ignorant; or at most, can only find in its circumstances some analogies, such as may justify and support a few vague conjectures respecting it.

Temperature exercises an important influence on the gastric solvent. At the ordinary temperature of the atmosphere, the action of the gastric juice is scarcely perceptible, even when continued during many hours.† Lower degrees of cold suspend its action still more completely. Heated to the temperature of the body—namely, to about 100° Fahrenheit — it acts very energetically. A further accession of temperature at first increases, but soon injures, and finally for ever destroys, all its digestive powers. The precise point at which this change of effect occurs is not clearly known; but it is probably at or near 120°. The dried pepsine of the artificial digest-

* Here, again, the author thinks it better to subjoin in a foot-note the successive additions to our knowledge that have gradually built up the brief statement of the text,—to which many readers will probably prefer limiting their attention.

As before mentioned, Reaumur, Spallanzani, and Carminati, may be regarded as having collectively determined that the gastric juice is an acid, antiseptic liquid, secreted on the introduction of food, and capable of dissolving certain alimentary substances, even when removed from the body.

The first attempt to analyze the organic matters of the gastric juice was made by Tiedemann and Gmelin (*Loc. cit.*). They announced the presence of mucus; an alcoholic extract or osmazome; and a substance, soluble in water and precipitated by various metallic salts, which they stated to be *Ptyaline.*

Eberle (Physiologie der Verdauung, Wuerzburg, 1834) adopted a more synthetical method of inquiry. He found that the addition of dilute acids to an infusion of the gastric mucous membrane formed an artificial digestive fluid. Schwann (Mueller's Archiv. 1836. pp. 70. *et seq.*, 90. *et seq.*: and Poggendorff's Annalen, Bd. xxxviii. p. 358.) went still further. He found that it was only the glandular part of the stomach which possessed this power. And by previously removing the albumen of a gastric infusion, and neutralizing its acid, he was enabled to precipitate with bichloride of mercury a substance, which, when mixed with very dilute hydrochloric acid, and freed from this metal, formed a powerful digestive agent. He therefore named it *Pepsine.* Wasmann (*Loc. cit.*) adopted a different method. He precipitated a very carefully prepared watery extract of stomach with acetate of lead or bichloride of mercury. After removing the metal and acid, he threw down the pepsine by alcohol, and thus purified it from osmazome, which is soluble in this liquid.

The various observers who have since corroborated Wasmann's statements do not seem to have effected any important improvement in this process. Amongst these we may enumerate Pappenheim (Zur Kenntniss der Verdauung, Breslau, 1839), Valentin (Repertorium, B. i., s. 64.), Elsaesser (Magenerweichung der Saeuglinge, Stuttgart, 1846), Buchheim (De Albumine, Pepsino, et Muco. Lipsiæ, 1845), Vogel (*Op. cit.*), Lehmann (*Loc. cit.*), Scherer, Stannius, and many others.

† *Op. cit.* p. 785.

* In the foot-note to this page.

† Beaumont, *Op. cit.* p. 146.

ive fluid will, however, sustain a temperature of 160° without damage. But at a heat above this, it becomes wholly inactive, and partially insoluble. And Dunglison* found the organic principle of the gastric juice to be insoluble in hot water.

Alcohol, acids, and alkalies, when applied in excess, have also a destructive influence on the digestive power of pepsine.

In the case of acids, this injurious effect is much less marked. As might have been expected from the constant reaction of the gastric juice, an acid is essential to its digestive efficacy;—indeed, we might almost say, to its very existence. Even that incomplete loss of acid, which we have seen to be involved in the precipitation of its pepsine, must be compensated by an artificial acidulation, before the aqueous solution of this substance regains its former digestive powers.

Here, however, as in the case of heat, it is necessary that certain limits should be observed. Wasmann found that an addition of about 3 parts of hydrochloric acid per 1000 formed a tolerably effective fluid:—a quantity which corresponds with about half of that present in the gastric juice according to Bidder and Schmidt's analyses.† But much larger proportions of this acid may be added, not only with impunity, but even with advantage. Thus Schwann used from 6 to 12 parts per 1000. And Elsaesser thinks that the most favourable proportion for digestive purposes is about 3 or 4 per cent. of muriatic acid:—a quantity which would be about five times as great as that present in the gastric juice.

But the nature of the acid seems a matter of indifference.‡ Nitric, phosphoric, sulphuric, acetic, and lactic acid, have all been successfully made use of. And the range of amount already specified for hydrochloric acid might, *à priori*, prepare us for the fact, that the requisite quantities of each of these acids seem solely related to their more or less dilute state; and do not allow us to recognize any trace of an equivalent chemical proportion.

Applied in still larger quantities, all of these acids first weaken, and then destroy, the digestive power of the solution of pepsine. The comparative amount of injury inflicted by equal quantities of the different acids appears to depend, like their solvent efficacy, chiefly on the degree of their concentration, and that of the digestive fluid itself.

How essential its acid is to the solvent powers of a natural or artificial gastric juice, is well shown by the effect of neutralizing it with an alkali. Under these circumstances, not only does it lose all action upon albuminous substances, but if mixed with them, soon shares in the putrefaction which they are liable to undergo. An equally rapid putrefaction occurs in the simple aqueous infusion of stomach. Left to itself, however, the powers of the neutralized gastric juice are only suspended; and can be restored by the addition of a proper quantity of acid. But in the course of time, the neutral fluid gradually becomes mouldy:—a process which appears to differ in its rapidity only from the similar decomposition that occurs in pure gastric juice, apparently after the slow evaporation of its acid.* A still larger quantity of alkali permanently destroys all its solvent powers, and is followed by its rapid putrefaction.

That incomplete loss of acid which was noticed as occurring in the ordinary processes for obtaining pepsine, does not entirely suspend its specific action. On the contrary, its watery solution still retains the power of precipitating large quantities of casein, and even of exerting a feeble digestive or solvent influence.

But while all such observations on the artificial digestive fluid agree in representing an acid as one of its most essential elements, some physiologists have gone further, and have asserted it to be so far the true and only principle of the gastric secretion, as to be capable of imitating its action. And others, who allow that the dilute acid is only rendered efficacious by the presence of the organic matters with which it is combined, have doubted the specific nature of the gastric principle; and have asserted that acidulated saliva or mucus, or an acidulated infusion of bladder, diaphragm, trachea, or intestine, is capable of effecting a solution of the protein compounds like that seen in artificial digestion. Each of these remarkable statements demands a passing notice.

Many dilute acids—such as sulphuric, nitric, acetic, hydrochloric, and phosphoric—can certainly produce appearances resembling imperfect solution, in meat and many of the protein compounds. But such a solvent action, even when most marked—as in the steeping of small pieces of coagulated albumen in dilute hydrochloric or phosphoric acid—differs greatly, both in nature and amount, from the true stomach digestion. It requires the aid of a much higher temperature; it is excessively slow, superficial, and imperfect; and the resulting weak and turbid solution often parts with its dissolved constituents on the addition of the ordinary reagents.

The same statement will apply to various experiments that have been made with an acidulated infusion of large or small intestine; in which the process of solution, though somewhat † more energetic, is still so feeble, slow, and imperfect‡, as to be scarcely comparable with that effected by the gastric juice. While we ought not to forget, that the superior

* Beaumont, *Op. cit.* p. 69.

† The acid Wasmann added to the pepsinous fluid being liquid, would contain less than half its weight of true hydrochloric acid.

‡ Bernard, *Loc. cit.*; Lehmann, vol. ii. p. 50.

* Beaumont, *Op. cit.* p. 71.; Blondlot, *Op. cit.* p. 351.

† Compare Valentin, vol. i. p. 366.; Todd and Bowman, vol. ii. p. 203.; and Frerichs, p. 795.

‡ In any future observations of this kind it would be very desirable to institute a strict comparison between the reactions of the resulting solution, and those of true peptone or albuminose.

efficacy of such infusions, and especially that of the duodenal membrane, is at least partially explained by the way in which the gastric juice is necessarily diffused, with the food, over the surface of the intestinal canal.

The effect of the neutral salts on artificial digestion has scarcely been investigated with all the attention it merits. But it appears not improbable that many of these inorganic substances assist solution, when present in small quantities, but oppose it when added in excess. This is especially the case with chloride of sodium, the ordinary condiment of mankind and of many animals. The effect of this salt in facilitating the digestion of albumen, fibrine, and casein, has been verified by Lehmann for the proportion of $1\frac{1}{2}$ per cent.

The effect of alcohol is also regulated by its amount and concentration. Diluted, it seems to have no chemical action whatever. In larger quantities, as before remarked, it precipitates pepsine. And in still greater excess, it permanently destroys all its digestive energy.

The way in which the process of gastric solution, whatever be its nature, is assisted by the minute division of the substances submitted to it, as well as by the movements of the stomach, is too obvious to require any special mention. It only remains to add that, according to Purkinje and Pappenheim, an increase in the amount of the atmospheric pressure furthers the artificial solution of albuminous substances. These observers therefore regard natural digestion as somewhat aided by the pressure of the gastric and abdominal parietes.

The quantitative relations between this organic principle and the proteinous substances which it dissolves, form a very important subject for inquiry. An exact determination of the quantity of pepsine which these substances require for their solution, would greatly assist us in solving many problems with respect to the chemistry of digestion. Or conversely, a knowledge of the exact numerical details of nutrition, and of the daily gastric secretion, would enable us to calculate the proportionate quantity of pepsine periodically required and used. But it is obvious that such calculations can only confirm direct observations; that they multiply all the known errors of their elements, and neglect their unknown ones. And the estimates derived from actual experiment are very conflicting: — if, indeed, they can be considered really comparable. Thus that precipitation of casein, which is effected by the watery extract of stomach, is producible, according to Mitscherlich*, by a quantity of pepsine amounting to $\frac{1}{500000}$th of the milk made use of: while Schwann states $\frac{1}{2000}$th to be required. Wasmann found that dilution of the pepsine to $\frac{1}{60000}$th did not destroy its power of dissolving coagulated albumen. Frerichs† and Schwann give estimates, which (allowing for the impurity of the extract of stomach) may probably be regarded as an assertion,—that one part of pepsine will dissolve 500 of meat, or moist and finely divided albumen. With these statements may be contrasted those made by Beaumont, Blondlot, Lehmann, and Schmidt. In describing his observations conducted with gastric juice, Beaumont* implies that this secretion cannot take up more than 50 per cent. of roast meat. From what he says, however, as well as from some observations by Blondlot†, it seems very doubtful whether even this can be regarded as a perfect solution. And Lehmann would fix its solvent properties at about 25 per cent. for moist albumen. While the average and maximum power of Bidder and Schmidt's pure gastric juice is stated by them at what would be about 10 and 20 per cent. respectively for the same substance. Reducing gastric juice to pepsine in accordance with their analysis, it would seem that one part of the organic principle cannot dissolve more than 12 of albumen. And even Beaumont's highest estimate would but raise these 12 parts of albumen to 30 of the more digestible meat:— a quantity which is still small enough to form a striking contrast with the larger proportion deducible from the statements of Frerichs. But it is scarcely necessary to observe, that the state of the substances used, the dilution of the fluid, and the amount of acid, will always exercise a great influence on the results; and may at least partially account for these great discrepancies.

As already implied, the gastric juice is capable of dissolving, not only albumen, but the protein-compounds generally, including in this term the various substances known by the names of fibrin, casein, globulin, vitellin, hœmatin, &c. To these we may add gelatin, chondrin, and gluten. In the case of all these, however, their physical condition seems greatly to regulate the rate of the process: density and bulk rendering it very slow; while, conversely, it is accelerated by minute division. Nor is it impossible that the quantities of the solvent required vary with the nature and aggregation of the particular substance. But in any case the ultimate effect is the same—the production of a complete solution.

The application of the term "chyme," by the older authors, to the food which had undergone stomach-digestion, sufficiently indicates that the mass possesses a comparatively uniform physical appearance. And even when further observation pointed out, that the chyme was liable to considerable variations in colour and consistence, the above opinions as to its uniformity required but a partial modification. For physiologists then began to be aware, that the gastric change was not so much a stage in the digestion of the whole of the food, as the solution of a certain class of its

* Bericht, &c. der Akademie der Wissenschaften zu Berlin, 1842, p. 147. *et seq.*

† *Op. cit.* p. 794.

* *Op. cit.* p. 133.

† *Op. cit.* p. 264.

constituents. It was reserved for Mialhe* to show, that the homogeneous physical constitution, which the whole contents of the stomach were erroneously supposed to assume at the end of its digestive act, is true in a much more important chemical sense, if limited to certain portions of the food. He found that the gastric digestion of the various protein compounds affords a solution which, whatever the nature of the substance originally dissolved, possesses the same physical and chemical properties:—these properties being due to its containing a substance which, from its relations to albumen, he called *albuminose*. Lehmann †, who has confirmed and extended Mialhe's researches, proposes for this substance the better name of *peptone*. ‡

Peptone.—According to these observers, the following properties are common to all kinds of peptone, from whatever substances they may have been derived. Reduced to the solid form by careful evaporation, peptone is a white or yellowish-white substance; almost tasteless and inodorous; very soluble in water; but insoluble in alcohol of 83 per cent. Its watery solution reddens litmus; and is precipitated by chlorine, tannic acid, and metallic salts; but is unaffected by boiling, by acids, or by alkalies. With alkalies and bases it forms very soluble neutral compounds or salts. An aqueous solution of these is still less precipitable by reagents than one of peptone itself. Thus it is thrown down only by tannic acid, bichloride of mercury, and a mixture of the acetates of ammonia and lead:—the acetate of lead, and the ferrocyanide of potassium causing but a faint cloudiness; and even concentrated acids, nitrate of silver, and alum, having no effect.

The ultimate chemical composition of any particular peptone so closely resembles that of the substance from which it is formed as scarcely to require any further remark.

In speaking of these chemical phenomena of stomach-digestion, there remains but to notice, that the addition of water, or a small quantity of fresh acid, is capable of restoring some of its original digestive powers to saturated gastric juice, or a solution of peptone. The degree in which this renovation can be effected is obviously a question of great importance. But at present there are no exact observations on which to found any conjectures respecting it. It seems, however, sufficient to explain the discrepancy previously alluded to § between the quantity of hydrochloric acid which is present in the normal gastric juice, and that which is required to be added in preparing an artificial digestive fluid of maximum solvent power.

The foregoing brief summary of the chief physical and chemical properties of the gastric juice, naturally leads us to the important question—What is the nature of its action?

1. It is obvious that the phenomena of gastric digestion do not constitute a simple process of solution by a dilute acid. For the organic principle is essential. The substances are not merely dissolved, but exhibit altered reactions. And, finally, they are not restored to their original form by the neutralization of the acid.

2. Some have supposed that the organic principle exercises a contactive influence, like that of spongy platinum in the acetification of alcohol.

3. Others have imagined that it produces a fermentation, like that excited by yeast in a solution of sugar.

But we have seen that gastric juice will not dissolve more than a certain quantity of protein-compounds. While, in both of the above processes, a small quantity of the contactive or fermenting substance excites an action, which continues until the whole mass has been oxidized or fermented, as the case may be. This objection appears fatal to both these theories. And as regards the latter of them, we may further point out, that, unlike the particles of yeast, which are themselves undergoing metamorphosis, those of the digestive fluid are singularly stable, and enjoy a singular immunity from the putrefactive process.

4. Schmidt * has propounded a fourth theory, according to which the organic principle, and the acid, of the gastric juice are united to each other in the form of a complex acid, which he calls the *hydrochloro-pepsic*. This is decomposed by heat into pepsine and hydrochloric acid. In the stomach it unites with protein-compounds as bases, to form soluble combinations. When treated with an alkali its pepsine is precipitated. And even when saturated with a protein-compound the power of the gastric juice is restored by fresh acid; because the latter, by uniting with the base, sets free the hydrochloro-pepsic acid, and thus enables it to combine with another portion of proteinous substance.

But in respect to the two latter statements, it would appear that an alkali precipitates from the gastric juice but a very small part of its pepsine; and that even this portion is in combination with calcareous salts. While the reactions of peptone show that the original pepsine is neither present as such, nor is capable of being set free from its state of combination by the addition of an acid.

And other facts, which seem to speak strongly in favour of this view, will as little bear a close investigation. Such are the close union of the acid to the organic principle; the definite amount of acid required for artificial digestion; and the similarly definite amount of proteinous

* Journal de Pharmacie, t. x., pp. 161. *et seq.*

† *Op. cit.* vol. ii. p. 50.

‡ Both names being comparatively recent, there can be little objection to the adoption of the preferable one. And "*peptone*" not only connotes its relation to digestion, but avoids the disadvantage of "*albuminose*":—viz., that of giving an undue prominence to the connection of albumen with the gastric function.

§ See p. 334.

* *Loc. cit.*

substances which the gastric juice will dissolve. For the more abundant of the salts contained in the gastric juice appear to be almost as closely united to its pepsine as is the acid itself. The supposed complex acid has never been isolated; still less has its combination with the supposed base. The latter, again, does not saturate the acid, and has never yet been replaced by other bases. In like manner, the tolerably fixed proportions of acid and of protein cannot be reduced to definite equivalents. And, finally, while the restorative action of fresh acid cannot be fully explained, the equally marked effect produced by pure water is still more mysterious.

We are thus gradually led to the conclusion, that neither of these four theories — solution, combination, contactive excitement, or transferred metamorphosis — will afford an adequate explanation of that process of stomach-digestion, from the observed phenomena of which they all so widely differ. It is indeed scarcely to be wondered at that we are unable to form a satisfactory theory. For it is probable we are still ignorant of many processes of organic chemistry. While it is possible that the action of the gastric juice is quite *sui generis*. And hence any view which unites most of the circumstances of the case, will be certainly as useful, and probably as true, as one which, like each of the preceding, assumes an undue parallel for the sake of a full explanation.

If we must connect the above details by some theory, we may first remark, that the gastric juice dissolves protein-compounds; that it renders them highly soluble; and that it assimilates their form and reactions to its own, without changing their composition. For any parallel to such a process we can only look to those lower degrees of chemical action, where solution and combination, adhesion and affinity, may be supposed to meet and merge into each other; where proportions are tolerably definite, but true equivalents indistinct; and where, though form is changed and reactions modified, elementary composition remains little affected. Actions of such a kind may be found in the union of many substances with water, or its elements, to form the compounds called hydrates. And the conversion of protein into peptone, by the gastric juice, presents so many analogies to the formation of a hydrate*, that it seems not impossible the chief office of this secretion may be, that of enabling water to combine with the various members of the albuminous groups of alimentary substances, in order to their acquiring that solubility, and uniformity of constitution, which must probably precede their admission into the current of the blood. To this vague indication of a theory, I will only add, that the mode in which a definite quantity of the organic principle takes part in such a process cannot even be conjectured. Its action certainly appears no way comparable to the effect of diastase on starch, or of emulsine on amygdaline. It seems to be an assimilation, in the strictest chemical sense. It is not impossible that the acid commences the process by a slight, though genuine, solution of the more resisting substances. And at any rate, this constituent seems to have the power of checking putrefaction, if not of arresting all metamorphosis, in the other ingredients of the secretion:—like the small quantity of oil of vitriol which is added by the chemist to hydrocyanic acid with the same object.

Process of secretion.—The process by which the gastric juice is secreted from the mucous membrane of the stomach, forms one of the most interesting problems in physiological science; and one which, if satisfactorily explained, would probably throw much light on the morphology of secretion generally.

Ever since the discovery of the stomach-tubes by Dr. Sprott Boyd, it has been generally assumed that the secretion of the gastric juice is mainly effected by a discharge of their glandular contents. The precise mode of this expulsion seems usually to have been left undecided: though it has been implied that the pressure of the muscular contractions of the organ upon the more or less solid food would almost compel an evacuation of the tubes. And more recently, Frerichs has asserted that the act of secretion is really aided by such an expulsion; and that the food becomes enveloped in a layer of the large gastric cells, the discharge of which from the stomach-tubes leaves them collapsed and empty.

To all of these statements the author ventures to offer a deliberate contradiction. In researches upon this organ which have extended over some years, he has never seen these gastric cells free from the tubes except when there was good reason to attribute their expulsion to mechanical violence. They are never present in large quantities. In the majority of examinations they are almost absent. With the proper use of the precautions previously alluded to, they will rarely or never be found. In addition to this, it may be added, that the arrangement seen in the Dog—where the stomach-tubes are lined by a continuous tube of epithelium, which is prolonged into the layer of columnar cells that occupies their intervening ridges—renders it almost impossible that these cells should be shed in their original form.

Another part of this statement has already been contradicted. During every stage of gastric digestion, the tubes may be seen with precisely the same form, size, arrangement, and contents, which they exhibit during the fasting state. This remark even applies to that narrow calibre of epithelium, which is seen within the axis of the proper gastric tube in the Dog. And hence, ignorant as we are of the exact mechanical arrangement of the fibre-cells at the bottoms of the tubes, still the excessive delicacy of these secreting organs, taken in conjunction with this uniformity of appearance, renders it highly improbable that they are evacuated by any extraneous pressure.

* Compare Dr. Prout's treatise "On Stomach and Renal Diseases," 5th edition, p. 470. *et passim.*

The anatomy of the fresh stomach also suggests other conjectures, which confirm the conclusion which we have deduced from the above sources. We have already noticed that, in the Dog, the columnar epithelium forms but a single row, and that it covers all the ridges during the digestive act. Hence the columnar cells can scarcely be stripped off in successive layers at this time. While the close attachment of each of these cells to those around it, together with their uniform appearance *in situ*, renders it alike improbable, either that a cell is extruded singly and then bursts, or that each, as it fills, ruptures and collapses. All those within a tolerably wide circuit of membrane seem absolutely similar and coeval.

In some cases, however, the gastric juice does contain columnar epithelia mingled with the food. In the Dog, this appearance is unusual, and the number of such shed cells is small. In the Rabbit, their separation is more frequent and extensive. While in the Pig, it often forms a more or less continuous layer, which is almost moulded to the ridges of the stomach and the mouths of its tubes*, and leaves the mucous membrane below denuded of this its proper covering. But it remains for future researches to show, whether this appearance is due to mechanical violence; to commencing putrefaction; or to the disturbances implied in the muscular contraction, the exsudation, and the other incidents of the act of death.

And whatever the interest attaching to such a dehiscence of these columnar cells, it can scarcely have any but a very indirect relation to the healthy secretory process that obtains in the living man or dog, in whom the pure gastric juice is completely structureless. This fact, announced by Beaumont, at a period when microscopy was much less understood than at present, has since been repeatedly confirmed in observations on gastric fistulæ which have been instituted by Blondlot, Bidder, Schmidt, Huebennet, and myself. And if great care be taken not to disturb the surface of the mucous membrane, we may often verify it in the fresh stomachs of dogs which have been killed immediately after feeding.

Here again we may refer to Dr. Beaumont's numerous observations.† He made use of magnifying glasses, by the aid of which he could distinguish the spheroidal glandular follicles, and the papillæ situated in their interstices. These papillæ, or *villi*, he found to be scarcely visible until food was applied to the mucous membrane; when they underwent a kind of erection, and protruded from its surface in the shape of small sharp processes. From these, according to this faithful observer, the gastric juice appears to exsude. Its secretion begins by the gradual appearance of innumerable lucid specks, which are smaller than the mucous follicles. These specks or points rise through the transparent mucous coat: and seeming to burst, discharge themselves upon the very points of these vascular papillæ, as a thin, transparent, colourless, limpid, acid fluid; which collects in small drops, and spreads over the whole gastric surface.

So thoroughly persuaded was Dr. Beaumont that the fluid exsuded from the papillæ alone, that he had not the least doubt the excretory ducts of the follicles were enclosed in these villi, and terminated in the lucid specks just alluded to; although he admits that he could not see any apertures here.

Comparing this description with what we now know respecting the anatomy of the mucous membrane, it is difficult to avoid coming to the conclusion, that the large and numerous capillaries beneath its ridges are in some way intimately connected with the secretion of the gastric juice. And whether this conjecture be right or wrong, the characters of this secretion corroborate the conclusion already deduced from the anatomy of the dead stomach: — viz. that the gastric juice is not composed of a shed epithelium. In like manner, the rapidity with which it exsudes seems to contradict any theory of even the most rapid solution of columnar* cells. And since anatomy shows that, until the end of gastric digestion, these cells, if dissolved, are immediately replaced by others, it follows, that to assume such a process of dehiscence would imply a rapidity of growth and organization, such as has never yet been verified in the higher Vertebrate animals.

The latter quantitative objection may be better carried out in detail. In Schmidt's experiments, a dog secreted $\frac{1}{20}$th of its weight of comparatively pure gastric juice in one hour. Transferring such an estimate to an average man of 140lbs. weight, it would follow that the human stomach, the whole mucous membrane of which scarcely weighs 4oz., can completely reconstruct its entire cell growth, — which is, at most, only half of this weight, — about sixty times in a single hour!

As regards the source of the acid, the above statement by Dr. Beaumont is supported by an interesting obervation of Bernard†; who finds that it is only the surface of the mucous membrane which exhibits an acid reaction, either in the digesting or fasting state. This statement I can confirm: al-

* Compare Koelliker, p. 150.

† *Op. cit.* pp. 95, 96, 128. *et passim.*

* When freed from their attachment, these columnar cells often undergo what seems to be a rapid solution in the surrounding fluid under the microscope. The first stage of this exhibits them as very delicate husks, which appear to have emptied themselves after losing the lid of cell-wall at their larger extremities. Their sides now often collapse: and increasing transparency soon renders them invisible. This process occurs so quickly as to resemble a digestive solution. But it is difficult to determine how far it is effected by the contents of the cell itself, apart from the surrounding fluid. A layer of mucus generally occupies the neighbourhood of any cut surface of gastric mucous membrane, and appears also to consist of the dissolved contents of cells.

† Gazette Médicale, Mars 16. 1844.

though I have sometimes found below the surface a faint acidity, such as might have been due to a mere admixture or imbibition of the fluids above.

But supposing Dr. Beaumont's conclusion true — that the gastric juice exsudes chiefly from the papillary ridges that intervene between the tubes — what office shall we assign to these latter structures themselves?

The occurrence of these tubes is the rule throughout the Vertebrate classes. And not only are the large cells which form their contents equally constant, but Goll and Koelliker's* researches have shown that it is in these cells,—or at least in that part of the stomach which contains them,—that the digestive power chiefly, if not essentially, resides. Any indirect or collateral action seems insufficient to explain such a close mutual association of structure and function :—an association which not only ranges a great part of organized nature, but repeats itself in the organ of the individual. Hence, whatever the office of these cells, it is probably concerned with the elaboration of at least one important constituent of the gastric juice. It would seem that this constituent is not the acid. Shall we therefore conjecture it to be the organic principle?

This conjecture, which rests on foundations so slight that the author feels he has no right to propound it, except in the interrogative form in which it presents itself to his own mind, is perhaps more compatible with the facts at present known than any other that he can indicate.

It is, however, possible, that the observation of Dr. Beaumont just cited was based on some optical illusion : — that, for instance, the lucid specks which he saw on the villi only, had in reality extended up these processes from dark and depressed openings of the tubes. But even supposing this to have been the case, the superficial acidity of the stomach may be regarded as showing, that the preparation of its secretion is only completed by the cell-growth which lines the lower part of the tubes.

At any rate, it seems certain that the gastric juice is not composed of the dehiscent nucleated cells of the mucous membrane of the stomach. This fact appears so well established, that we ought not to shrink from receiving it, however it may impugn what is ordinarily understood as the cell-theory. In respect to the latter doctrine, the author can only mention another view, which, though novel and plausible, he has long felt obliged to give up.

After verifying the obscure cytoblasts which fill the large oval gastric cells, and the more distinct ones which line the axis of the stomach tube†, as well as the gradual transition of these into the ordinary columnar epithelia covering the ridges,—it occurred to him that this structure, together with Bernard's and Beaumont's observations, were all susceptible of a single explanation. According to such a view, it might be supposed that the mother-cell gradually enlarged, ruptured, and discharged its contained cytoblasts. These arranged themselves in the axis of the tube; and urged by a gradual pressure, or by the growth of new cytoblasts below them, passed up the follicle to where the mother-cells ceased. There they became attached to the wall of the tube itself, and acquired a columnar form by a gradual distention of their interior;—a distention, which increased as they approached the summit of the ridge, where they were finally extruded, or burst. Thus the cell which was constructed below, was filled above :—a subdivision of the secretory process, which might be supposed to depend upon the solvent powers of the secretion being injurious, either to the production of blastema, or to the multiplication of cells. Such a view seemed more or less to account for the structure of the mother-cell; for the gradual transition of the cytoblast into a columnar cell; for the superficial acidity, and for the vascular arrangements, of the mucous membrane. It also appeared to be confirmed by the tendency of the columnar epithelia to cohere strongly with each other, and adhere slightly to the subjacent basement membrane. But the uniform anatomy of the ridges, and the completely structureless character of the gastric juice, were insurmountable objections, which ultimately led to the complete abandonment of this theory.

And as regards the whole theory of secretion by cells, surely it is high time to modify it so that it might involve, not a less immediate action, but a somewhat less extravagant expenditure, of these minute organs. For the improbability which we have shown to be implied in the application of this theory to the stomach, holds good in a far higher, not to say a very different sense, of many other secreting structures. Indeed in some of these, it is obvious, that their situation would involve an enormous waste of life and matter, supposing the bulk of their organic products to be really enclosed in deciduous or dehiscent cells. Amongst such we may specify the kidney, the most important duties of which are supposed to be executed by secretion into a cell-growth, from a venous surface — a cell-growth of which we may doubt whether it even undergoes a rapid solution, while we can definitely predicate that it is not discharged entire, in any quantity at all commensurate with the large amount of solid constituents which is removed from the body in the urine.

Small intestine.— The next portion of the alimentary canal is that which is included between the pyloric and ilio-cæcal valves, and is named, from its diameter, the *small intestine*

* *Op. cit.* Bd. ii. p. 146.

† It is interesting to notice the close structural analogy offered by these small axial cells to those which line the buccal and duodenal glands. The more so that the latter appear to secrete a fluid which possesses the capacity of effecting a rapid and important metamorphosis in another class of organic substances. (See p. 362.)

(Lat. *Intestinum tenue*, Fr *Intestin grêle*, Germ. *Duenndarm*).

The shape of all this portion is cylindrical. Its average length is about 20 feet; its diameter about 1¼ inches.* But apart from those varieties in its dimensions which it presents in different individuals, the yielding nature of the tube allows it to be narrowed by artificial extension. While, *vice versâ*, it is just as easily shortened by dilatation. And it is very difficult accurately to estimate those minor degrees of distention to which it is liable. Hence little stress can be laid upon the statement of Cruveilhier, that the small intestine tapers away from the duodenum to near its extremity, where it suddenly dilates to enter the large intestine.

The small intestine occupies the cavity of the belly. Its commencement, at the pyloric extremity of the stomach, is placed in the right hypochondrium; its termination, in the cæcum that begins the large intestine, occupies the right iliac fossa, to which this part of the intestinal canal is fixed. The few inches of bowel immediately above this extremity frequently occupy the pelvic cavity. But almost all the intervening portion is so free to move, that each particular point of its length may be found in any part of the abdomen or pelvis.

* Trustworthy observations on this point are still to be desired. Meckel states that the length of the whole intestine is from three to ten times the stature. And most authors have been content to follow him in estimating its average proportion as six times the height of the body. As I presume such a comparison of the two measurements was never intended to be more than an aid to the memory of the Anthropotomist, I need scarcely point out its inherent improbability, as well as the difficulty of establishing a close ratio between a multiple assumed to be so high, and a multiplicand known to be so variable. Besides, differences in the dimensions of the canal are not easily established, unless their amount is very considerable. For the facility with which, in such a tube, length is convertible into width, forms one palpable source of error, which can only be obviated by a very careful comparison of both the above measurements. The effect of a more or less complete removal of the mesentery is almost as obvious; and perhaps entitles us to suspect that all such estimates of the length of the separated bowel represent it as somewhat greater than it would be *in situ*. And we are still more unable to determine that alteration of both dimensions which the simultaneous dilatation or contraction of its two muscular strata would necessarily effect. While it is only after we have either obviated, or allowed for, all the preceding causes of inaccuracy, that we can come to any valid conclusion respecting those differences which doubtless obtain in different individuals.

The statement I have ventured upon in the text is based upon a number of measurements made by myself. In making these, the healthy intestine was laid upon a board, and spread out to what seemed a proper width, before taking its length. Their number (less than forty) is too small to justify us in regarding their average as a very valid one. They afford no information as to the effect of age or obesity. But they give what is probably a more accurate estimate than that ordinarily adopted by authors. And they agree with an average given by Cruveilhier, as well as with four cases, in which it seems not unlikely that he adopted precautions similar to those just alluded to.

The duodenum.—That upper part of the small intestine which is directly continuous with the stomach, is distinguished, both from this organ, and from the lower part, by certain peculiarities. And though these chiefly affect its external anatomy, still we shall hereafter find that they are not unaccompanied by differences in the structure of its mucous membrane. Starting from the constriction before alluded to, as marking the site of the pyloric valve, the intestinal tube forms a curve in the shape of a horse-shoe around the head of the pancreas;

Fig. 254.

Shape and arrangement of the duodenum. (The stomach and liver are raised to show the pancreas.)

st, stomach; *p*, its pyloric valve; *l*, liver; *g*, gall-bladder; *d*, duodenum; 1, 2, 3, its first, second, and third portions; *pa*, pancreas; *h*, head of the pancreas, which is received into the concavity of the duodenum; *sp*, spleen; *a*, aorta, behind the inferior transverse portion of the duodenum; *sm*, the superior mesenteric artery, in front of it.

receives the duct of this gland, as well as that of the liver; and is closely fixed by peritoneum to the posterior wall of the belly. This fixed commencement of the small intestine has been named the *duodenum*, in consequence of its length being estimated at twelve finger-breadths (δωδεκαδάκτυλον, *zwoelffingerdarm*). It has also been called the *ventriculus succenturiatus*, or supplementary stomach;—a vague term, which was probably based upon an inaccurate notion of its office.

Beginning at the pyloric constriction, the duodenum proceeds outwards, backwards, and a little upwards, to the under surface of the right lobe of the liver. It then turns downwards, and a little inwards, in front of the right kidney; so as often to impress a shallow fossa on the hepatic surface in front of that depression which corresponds to this organ. After a short perpendicular course, it finally makes a second bend, by which it regains a horizontal direction, and passes from right to left, and a little upward, in front of the vena cava, the aorta, the right crus of the diaphragm, and the vertebral column. It terminates opposite the left side of the body of the second lumbar vertebra, at a point which corresponds to the commencement of the mesentery. Here the intestine becomes free, and is named the *jejunum*.

The length of all this curve, when unfolded, is about ten inches. But for the sake of greater exactness, the three chief portions of the duodenum may be described separately.

The *first portion* is called the *superior transverse* or *hepatic*. It is much the shorter of the three, being scarcely two inches in length. It lies solely in the right hypochondrium; and, near the neck of the gall-bladder, terminates by bending downwards to merge into the second portion. Like the stomach, it is invested by peritoneum on both surfaces. This membrane is derived from the gastric omenta previously described; the extreme right of the gastro-hepatic omentum being sometimes called the *ligamentum hepatico-duodenale.* The latter fold of serous membrane also forms the anterior boundary of the foramen of Winslow, or opening by which the general sac of the serous membrane communicates with the bag of the omentum; and it contains the hepatic duct and vessels.

The above relations of this first portion of the duodenum to the peritoneum confer upon it a mobility which approaches that of the stomach; while its close proximity to the gall-bladder explains that discoloration by bile which is generally seen in the dead intestine,—as well as the adhesion and ulceration of its parietes, which so frequently occur in the course of disease of the liver or gall-bladder.

The *second*, the *descending* or *vertical portion*, which is rather less than three inches long, passes downwards, and slightly inwards, to the right side of the third lumbar vertebra. Above it is the right lobe of the liver. In front it is crossed by the right extremity of the transverse colon. Behind it is the inner border of the right kidney, together with a variable extent of its anterior surface, and its emulgent vein. On its right side is the termination of the ascending colon. On its left it is intimately connected with the head of the pancreas. Every one of these anatomical relations has more or less pathological importance.

The partial covering of peritoneum received by this portion of the duodenum may be traced, from the front of the great omentum, to the anterior surface of the intestine; and around its external or right side, to the wall of the abdomen. Here it is fixed to the right kidney, by an attachment that is sometimes termed the *ligamentum duodeni renale.* The posterior and left surfaces of the intestine, which are devoid of this serous membrane, are connected with the neighbouring organs by a loose areolar tissue, that concedes to the tube a considerable degree of distention and movement.

The *third or inferior transverse portion* is about five inches in length. In its course across the spine it lies upon the structures already named. Above it is the lower border of the pancreas. In front of it is the posterior or attached border of the transverse meso-colon,—the superior lamina of which covers it above, the inferior below, so as to leave an uncovered space along the line of their bifurcation. Anteriorly to this double process of peritoneum, is the large and moveable transverse colon which it serves to attach. And close to the commencement of the mesentery the end of the duodenum is crossed by the superior mesenteric artery and nerves.

Owing to this very partial covering of serous membrane, the inferior transverse portion of the duodenum is even less mobile and dilatable than either of the preceding. And, from the position of the pancreas above the intestine, distention of the latter chiefly affects its inferior surface, which may thus be rendered so convex and bulging as to cover the aorta to within a very short distance of its bifurcation.

Hence the duodenum becomes most fixed in the second and third divisions of its course. Its fixation and curvature may together assist in delaying the passage of its contents, and in facilitating that admixture of the biliary and pancreatic secretions to which its attachment perhaps chiefly refers. Its use as a means of fixing the stomach has already been sufficiently alluded to. Its comparative immunity from hernia is explained by its site.

The *jejunum* and *ileum.*—Below the duodenum, the small intestine is loosely attached to the posterior wall of the belly by means of a double lamina of peritoneum which is called the mesentery (*μέσος middle, ἔντερον intestine.*) Behind, this fold is fixed to the cellular tissue that covers the aorta and vena cava, by a line of attachment which is not quite vertical, but descends from the end of the duodenum to the commencement of the cæcum, passing very obliquely across the spine from the left to the right side of the lumbar vertebræ. In front, its two laminæ split to enclose the bowel, around which they become continuous with each other. Its antero-posterior depth between these spinal and intestinal borders is about three or four inches; but tapers away suddenly at its commencement and termination. We may, perhaps, gain a better idea of the peculiar shape of this process of peritoneum by imagining it as a very obtuse triangle of some flexible material. Such a triangle we may suppose fixed to the spine by a truncated apex of three inches in length. While its broad base, which is about twenty feet long, is attached to the intestine, where it is plaited so as to occupy the least possible space.

It is the extreme freedom of movement which such a mode of attachment concedes to the small intestine, that gives rise to the convoluted appearance so characteristic of this part of the tube. The exact figure of these convolutions is probably never quite alike at any two different times in the same individual,—being the conjoined result of the muscular movements of the canal, the nature and amount of its contents, the size of the neighbouring viscera, and the state of the abdominal parietes. The effect of dilatation resembles that seen in some other parts of the alimentary canal:—namely, distention of the tube always causes it to split up the loosely connected laminæ of peritoneum, and extend backwards between them, so as to shorten the length of its tether of mesentery.

The terms *jejunum* and *ileum* refer to a division of the small intestine which, though to some extent an arbitrary one, is not only too convenient to be altogether dispensed with, but is also connected with certain peculiarities in the structure of the mucous membrane, that will be hereafter alluded to. The jejunum includes the upper two-fifths, and the ileum the lower three-fifths, of the small intestine.*

Muscular coat.—The muscular coat of the small intestine consists of the fibre-cells previously described, the bundles of which are arranged in two layers,—an outer or longitudinal, and an inner or circular. The first constitutes a very delicate lamina, which is often scarcely visible at the mesenteric border of the tube, but is thickened at the opposite margin, where it is firmly united to the peritoneum. The circular fibres form a much stronger and more perfect stratum; and many of their bundles, like those of the same layer in the stomach, seem to take a slightly oblique direction; so as to join with others above and below them. Both layers (and especially the transverse) are somewhat stronger at their commencement in the duodenum. But from the middle of the jejunum their thickness remains unaltered throughout the rest of the small intestine.

Movements of the intestine.—The muscular actions of the intestine have long been reduced to two:—a normal *peristalsis*, which urges the contents forwards towards the anus; and an abnormal *antiperistalsis*, by which they are propelled backwards towards the stomach. But each of these movements has rather been maintained as a doctrine, than verified as a fact.

From the mere tenuity of the muscular coat of the small intestine, we might infer that its movements are much less vigorous than those of the stomach and œsophagus, in which this tunic has a thickness from two to six times as great. Indeed, an active and continuous peristalsis, like that which may be seen in these segments of the canal, would scarce allow the time necessary for the digestive act. Even a slow progressive contraction of two inches per minute would traverse the whole length of the intestine in from two to three hours:—a speed which we have every reason to believe very unusual in the healthy subject.

To obtain direct evidence respecting these movements, various methods have been resorted to.

In the healthy living intestine, it is but very rarely that any definite muscular action can be seen or felt through the wall of the belly. In some of the Polyps, however, the alimentary canal appears to exhibit a peristaltic, but intermittent, movement. And in Man, the *borborygmi* which sometimes occur in conditions but little removed from those of health, constitute sufficient evidence of a valid intestinal movement. While in cases in which abnormal obstruction of the intestine has been followed by an accumulation of fluid in the segment above the occluded part, the wall of the belly often becomes so extremely distended and thinned, as to allow us to recognise a progressive rolling contraction of the dilated bowel. Such observations at least prove that its muscular coat is capable of very vigorous contraction, while in this state of undue distention.

When the intestines of a healthy living animal are exposed by vivisections, surgical operations, or accidental injuries, they are found at rest. Hence, could we implicitly trust these appearances, we should assign but a very slight mechanical value to the intestinal contractions. But such an estimate would obviously be at variance with that propulsion of their contents which we know them* to effect. And, apart from this implied contradiction, it is evident that such observations can never be regarded as affording us trustworthy evidence of what really obtains in the healthy uninjured animal. For not only is it possible that the slow and feeble contractions of the intestine are much interfered with by the pain and disturbance which such operations or accidents presuppose, but I would add, that there are considerable grounds for suspecting that irritation of the peritoneal tunic of the bowel can produce relaxation of its subjacent muscular coat.†

Until lately, it has been usual to augur the movements which occur during life, from an inspection of the intestines of healthy animals immediately after their death. On laying open the abdomen of a newly-killed animal, its intestines are seen lying perfectly still. But in a short time, those parts of them which are exposed to the air begin to experience vigorous contractile movements. In many instances, these contractions are irregular and undefinable, and are hence rather "vermicular" than "peristaltic." But in other cases, they take on appearances of a forward or backward course, or sometimes of each of these directions alternately. Where transverse constriction is marked, it almost always takes a direction downwards, or towards the anus; and is preceded by a dilatation which stretches the intestine to the full length of its mesentery. After a few minutes, the contraction of

* The former derives its name from the *jejune* or empty state in which it is usually found after death: and the latter either from its convoluted form (εἰλέω, *circumvolvo*), its being the most frequent seat of the disease called *ileus*, or its relation to the iliac bone (*os ilii*).

* It can scarcely be necessary to argue the question which has sometimes been raised:—namely, whether it is the muscular wall of the belly, or the muscular coat of the intestine, that propels the contents of this tube. For this is obviously an inquiry, which might be decided by a reference to its human and comparative anatomy, even in the absence of all direct observations as to the nature of its contractions, and their necessary mechanical effects.

† The effect of scratching the peritoneal coat (see opposite page) is perhaps partly due to an action of this kind.

the intestines generally gives them a nodulated or almost moniliform shape, and the movement gradually ceases. On uncovering portions of the canal hitherto concealed, all these appearances are repeated. The contracted state remains for some hours, and finally again disappears.

Now the tranquillity of these portions of intestine previously to the admission of air, the irregular and diffuse nature of the contractions themselves, the final result on the intestine, and the effect of uncovering fresh portions—all these circumstances together offer the strongest probability, that the movements witnessed are due to the contact of the air. And hence, although it is interesting to notice that these contractions often assume the form of a peristalsis (that is, of a circular constriction which travels slowly in a direction towards the rectum), still they do not warrant any conclusions as to the nature or force of those definite movements which are doubtless executed by the intestines during life.

Nor are the movements which result from applying a local irritation to the bowel, under the same circumstances, much more uniform or conclusive. Unless excited before the commencement of the vermicular movements, or towards their close, they are obviously liable to be confused with these;—which, indeed, they closely resemble. Thus, when the surface of the bowel is irritated mechanically, a mere local contraction is sometimes produced. In other instances, and especially when the duodenum is the part attacked, the contraction extends downwards, or even upwards, from the irritated point. Sometimes this diffused contraction occurs almost immediately after the application of the stimulus; sometimes only after the lapse of a considerable interval of time. Sometimes, without any repetition of the stimulus, such waves are repeated; with short intermissions, and of gradually diminishing strength. Sometimes, instead of one continuous wave, a broken or interrupted one is produced;—a condition which is chiefly seen in the small intestine. Similar contractions may also be excited by the mechanical or chemical irritation of the nerves which immediately supply the intestines. But irritation of the mucous membrane has little or no effect. Direct galvanic stimulation, by means of the rotary electro-magnetic apparatus, repeats many of these appearances. On applying the approximated electrodes to a given point, a short interval precedes the occurrence of a local contraction: and this contraction endures after their removal. In some animals, this local contraction is slowly propagated onwards, for a variable distance, towards the rectum. This continuous movement may even be repeated without any fresh application of the stimulus. But that more diffuse irritation which may be produced by stroking the intestine with the wires gives rise to none but local contractions. While galvanizing the nerves reproduces the lively, but general, movements above alluded to. And finally, whatever be the form of irritation, it ceases to have any effect, soon after the lapse of that period at which the vermicular movements usually cease. This departure of irritability may, however, be retarded by warmth, or by preventing the access of air. And the capacity for such movements may sometimes be restored by returning the divided and dead intestine to the belly of the living animal. Finally, though the repeated irritation of any one part soon exhausts its contractility, still, after a short interval of repose, it is at least partially restored.

On mechanically irritating the exposed intestines of the living animal, very different results are obtained. Compressing them between the fingers produces a local contraction, which lasts some few minutes, and then disappears. Scratching their peritoneal surface usually gives rise to elevations, which are just as local as the preceding depressions. These elevations,—which seem to be due to relaxation of the outer or longitudinal muscular layer,—are accompanied by contractions of the deeper transverse fibres. And the latter can still be excited, after all possibility of producing the former has been destroyed by cold. Mechanical or chemical irritation of the mucous membrane, or pinching or section of the nerves, produces no movements whatever:—even where the degree of nervous stimulation is such as to cause convulsive movements of the hind feet of the animal. And distention of the bowel with water seems to be equally inefficacious; indeed, it appears to leave the ordinary irritability by local stimuli very little affected.

The observations of Schwarzenberg and Ludwig *, upon dogs in whom intestinal fistulæ had been carefully instituted, afford much more direct and trustworthy evidence respecting the normal intestinal movements. They introduced into the canal balls of wax, attached to slender lead wires; and thus verified the following details. The contents of the canal are propelled by a slow continuous peristalsis, which has a definite direction towards the rectum. And although irritation always excites a local contraction, it only gives rise to peristalsis at definite times, during the intervals of which the intestine remains at rest. These times have a general connection with the digestive act: the period of minimum activity being before a meal; while the maximum of movement is usually from four to six hours after it. But the act of peristalsis is essentially independent of the presence of food; since it may be produced in a starving animal, or in an empty segment of tube. And not only does this intermittent character affect the general occurrence of the propulsive act, but even, to all appearance, its specific phenomena. For when applied at the proper period, a single continuous irritation produces a repeated and intermittent peristalsis. Hence it is obvious that, during

* Zeitschrift fuer die Rationellen Pathologie, Bd. vii. p. 315.

the short intervals of this peristaltic act, the irritation is incapable of exciting contraction.

We may perhaps sum up all these results as follows. Direct irritation of this mass of organic muscle excites loca contractions; which are of slower access, feebler power, and longer duration, than those of the striped fibre. Shortly after death, these contractions of the intestinal coat evince a general disposition to extend beyond the site of their origin. But during life, this tendency is so modified by some governing force, that, in obedience to the requirements of the digestive organ, it is either exalted into a definite and effective peristalsis, or altogether suppressed. This definite peristalsis forms the ordinary muscular action of the bowel; and is the chief agent in the proper propulsion of its contents. As regards its intensity, we can only conjecture that it is scarcely more than sufficient to propel the normal contents. As respects its character, it is essentially intermittent. As to its extent, it seems to traverse long segments of the tube. But it remains very doubtful whether every — or indeed any — contraction proceeds continuously throughout the whole length of the intestine. Finally, we have a right to suppose, that at least the more active forms of peristalsis have in them so much of rhythm, as to be not only repeated, but self-repeating, at definite intermissions of time.

But the exact mechanism of this peristalsis remains in obscurity. Nay, more, the information at present at our disposal will not even enable us to take the first step in that process of induction by which alone it will probably be arrived at.

In his admirable Essay on Muscular Movement, E. Weber* has well illustrated the peculiar characters of the contractions which are excited by the irritation of organic muscle. He has shown that in the Tench (*Cyprinus tinca*), in whom the muscular coat of the intestine is composed of striped or animal fibre, galvanizing the chief nerves of the tube produces an immediate, powerful, and cotemporaneous contraction, in place of the slow, feeble, intermittent, and enduring action seen in the unstriped or organic intestinal muscle of the other Cyprinoid species. He has also found that the Iris of various animals repeats the same contrast of structure and irritability. Hence he argues, that the organic muscle is less directly influenced by the nerves; and that these are only connected with this contractile tissue in some such mediate way, as that by which irritation of the sensitive or afferent nerves gives rise to the reflex movements which are producible in voluntary or striped muscle.

But do these facts warrant such a conclusion? On the contrary, do they not render it more probable, that the above varieties of contraction are in some way inherent to the very structure in which these kindred animals differ, rather than that they are brought about by supposed differences of the nervous centres or trunks:—differences (by the way) such as the existing state of our knowledge would rather contradict than establish? In the intestine of a single Cyprinoid species, the fibre-cell gives place to the striped fibre. Hence, failing all proof of other differences, is it not precisely to this remarkable contrast of structure, that we must refer the parallel contrast which is observed in its contraction, when a stimulus is applied to its nerves?

This direct reference to the structure of the organic muscle seems to be most justifiable in the case of the local contractions above alluded to; many of the peculiarities of which are almost what might have been expected from the rudimentary structure, the little vascularity, and (especially) the mode of aggregation, of the fibre-cells. But as regards the less local contractions of the unstriped fibre, their tendency to peristalsis and intermission soon after death, appears to demand some wider and less continuous connection of different points and times, than the tissue itself would directly afford. Such a means of association suggests itself in the nervous system. And, since the removal of the mesentery does not deprive the contractions of this peristaltic character, any supposition of this kind would appear to refer it to the nerves within the walls of the intestine. But it is difficult to believe that these nerves have ganglia; nor have any of these essential elements of a nervous centre ever been seen in this situation. While it has been pointed out by Wild, that the excision of a portion of the œsophagus prevents all propagation of its peristalsis beyond the interrupted point: — a fact which tends to show that the contraction of each segment is in some way conditionated by that of its immediate predecessor. The latter experiment, however, supposes such a serious interference with the tube, that any negative result can hardly be regarded as conclusive. And hence, until future researches bring additional information respecting the ultimate distribution of the nerves of this unstriped muscular tunic, and the exact arrangement of its constituent fibre-cells, the relative share of the muscular and nervous tissues in these peculiar contractions can hardly be conjectured. The stimuli by which we excite them in our experiments are in reality far too rude, diffuse, and uncertain in their application, to afford much ground for a decided preference of either muscle or nerve, as forming the chief modulator of that contractility which is, no doubt, essentially inherent to the sarcous substance itself.

From the appearances noticed in the healthy intestine soon after death, it may be doubted, indeed, whether even this last phrase is quite specific enough; — whether we ought not to regard* contraction itself (rather than an abstract "contractility") as the inherent property of the living organic muscle. In the observations just mentioned, we have seen that the death of the animal was soon followed by an irregular, but distinct, contrac-

* Wagner's Handwoerterbuch der Physiologie.

* A contraction answering to what has been philosophically distinguished by Professor Bowman as "*passive*" in the case of the striped muscle.

tion of the unstriped muscular coat of its intestine:—a contraction which was apparently excited by the air, but was certainly independent of the nervous centres. This remained for a time, and then disappeared, never to return. Hence it seemed, in short, "a kind of precipitate *rigor mortis*, hastened by exposure to the air."*

The truth of this analogy between the unstriped and the striped muscle is confirmed by observations made on corpses in which all exposure of the intestine has been avoided until an hour or two after death. A comparison of such examinations would show that the death of the intestine, like that of the arteries, is accompanied by the access of a definite *rigor mortis*, which is closely analogous to the stiffening seen in the voluntary muscles. Both the access and disappearance of this contraction are, however, more rapid than in the striped fibres of the proper organs of locomotion. And its appearances are much less distinct. In the intestinal canal, it is chiefly recognized as a narrowing of the tube; which is attended by an increased thickness of its walls. But it is sometimes better evidenced by intus-susception of the canal; or by irregular contractions of its calibre.

But whatever the exact relation which the various contractions producible in the intestine bear to the specific structure that forms its muscular wall, it seems certain that the true propulsive peristalsis of the healthy living animal is a complex and co-ordinate act, which is at least indirectly dependent upon the cerebro-spinal centre. And Weber's experiments on the highly excitable intestine of the Tench point definitely to the medulla oblongata, as that segment of the nervous centre by which this connection is chiefly brought about. While, as might have been expected, numerous observations concur to represent the pneumogastric and splanchnic nerves as the channels by which this central organ influences the alimentary canal. But the exact degree in which the various vertebral and prevertebral centres of the sympathetic can transmit, modify, or originate the nervous changes which pass to and from the bowel, is at present utterly unknown. There are however various reasons for suspecting, that neither of the two main ganglia which intervene between any part of the intestinal surface and the cerebro-spinal centre, really limit the transmission of an afferent, or give origin to an efferent, change.

Anti-peristalsis.—The ordinary theory of intestinal anti-peristalsis may be thus stated. At a certain stage of an intestinal obstruction, the immoderate irritation which it implies reverses the natural peristalsis of the bowel; so that, instead of proceeding towards the anus, it passes in the contrary direction. In this way it impels the contents of the tube towards the stomach; whence they are vomited by the aid of an extension or reproduction of the same action.

About eight years ago, the author † was led to investigate this doctrine, until then universally accepted. He was thus led to the conviction, that it ought to be unconditionally rejected; that it was probably false; and certainly had never been proved to be true. The following were his chief reasons for coming to such a conclusion:—

1. It is difficult even to conjecture anything in the degree or kind of irritation present in intestinal obstruction, which should limit the occurrence of anti-peristalsis to this state. 2. Since the physical state of occlusion is the necessary condition of fæcal vomiting, it is probable that the causative process by which this occurrence is brought about must be physical also. 3. No anti-peristalsis has ever been observed;—the movements which occur in the obstructed bowel after death being similar in their nature to those witnessed in the healthy intestine under similar circumstances. 4. The whole of the appearances seen after death in the obstructed bowel, show that its contents have been propelled forwards towards the occlusion, and not backwards from it. 5. Distention of almost all the interval between the pylorus and the occluded part appears to be a condition of fæcal vomiting;—so much so, that the date of access of this symptom roughly indicates the locality of the obstruction.

Hence, instead of an imaginary anti-peristalsis, the author ventured to propose a theory which seemed to deduce the process of fæcal vomiting from the ascertained conditions of its occurrence.

The complete obstruction of the intestinal tube at any point, gives rise to an accumulation of its contents above the seat of the structure. This gradual distention of the bowel is accompanied by an active propulsion, which may often be seen and felt through the wall of the belly, as a violent writhing peristalsis. After a variable period, vomiting either occurs for the first time, or if already present from other causes, it becomes fæcal. But peristalsis in an obstructed tube distended with fluid, not only implies a forward movement in the particles that occupy its periphery, but also necessitates more or less of a backward current in those which are situated in the axis or centre of the canal. And the uniform consistence of the distending fluid, or the return of solid fæces, through many feet of tortuous bowel, into the upper part of the canal, constitute frequent phenomena, which are best explained by the mixture and circulation that these two currents must tend to establish. On the fæcal fluid reaching the stomach, vomiting is excited. And it is scarcely necessary to add, that this latter process, as usual, involves the more or less complete evacuation not only of the stomach, but also of the upper part of the distended small intestine.

Mucous membrane.—Having thus briefly described the peritoneal and muscular coats of the small intestine, we may next proceed to consider its mucous membrane:—the structure on which its various functions essentially depend.

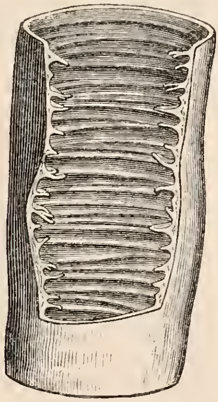
* Author, *op. cit.*

† *Op. cit.*

This tunic everywhere consists of the ordinary elements of a mucous membrane: — namely, a basement membrane, an epithelium, and a layer of areolar tissue that contains an admixture of the muscular fibre-cells. But, instead of forming a simple, flat expanse, it undergoes numerous modifications; which, under the names of *valvulæ conniventes*, *intestinal tubes*, *villi*, *agminate follicles*, *solitary follicles*, and *racemose glands*, will especially claim our notice.

Valvulæ conniventes. — Almost all the small intestine is complicated by the presence of transverse folds of mucous membrane; which project from its inner surface into its cavity. These projections, which were known to many of the earlier anatomists, were named by Kerkring the *valvulæ conniventes*;—apparently from his thinking that they delayed the intestinal contents, but still as it were, connived at their passage. They begin in the second portion of the duodenum, and only cease in the lower fifth or sixth of the small intestine. They are best shown by moderate distention of the tube with alcohol; which slowly hardens them, so that they retain their shape, even after a portion of the wall of the bowel has been removed to display its interior.—

Fig. 255.



Small intestine distended and hardened by alcohol, and laid open to show the valvulæ conniventes occupying its interior. (From a preparation in the Museum of King's College.)

Extreme distention greatly diminishes their size, but never effaces them altogether. And such a permanent character sufficiently distinguishes these folds from those temporary creasings which are seen generally throughout the stomach and intestine, and which are sometimes spoken of as preceding them in the first part of the duodenum. At first they are very small and scattered, rise little above the general mucous surface, extend but a short distance across the tube, and break up at their extremities into still more minute creases, which often pass obliquely to join those next them, above and below. In the lower part of the duodenum, they gradually acquire a number and size, which are retained throughout the whole of the jejunum. But from the beginning of the ileum, they again diminish; first in frequency, and latterly in length and depth. And in the lower third of this segment, they generally disappear altogether.

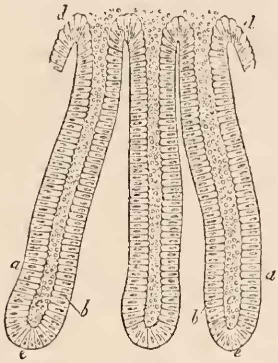
Each of these folds consists of a duplicature of mucous membrane, enclosing a process of the loose areolar tissue which everywhere separates the mucous from the muscular coat. Opposite the attached border of the *valvula*, this layer is somewhat thicker; but does not appear to contain more than its ordinary small quantity of fibre-cells. The process which it gives off to each of the folds contains vessels, nerves, and lacteals. The relation of this tissue to the *valvula* is well shown by the result of its inflation; which produces a kind of artificial emphysema, that completely obliterates the whole projection. When the cavity of the intestine is forcibly distended, the *valvulæ* are placed vertically to the general surface. But in the ordinary state of the bowel, they are easily moved by any external force; so that their free margin is generally directed obliquely upwards or downwards. Their direction is nearly transverse to the axis of the tube. Their variable extent around the wall of the bowel forms one-half, two-thirds, or even three-fourths of a circle. Their greatest projection occupies the middle of their length, where they are often from one-fourth to half an inch deep. But towards either extremity, they gradually sink into the general mucous surface. In doing this, the valves usually swerve a little from their hitherto transverse and parallel course; so that each joins by one or both ends with the fold immediately before or behind it. And sometimes a bifurcation of the tapering fold unites its extremity to two of its neighbours.

The office of these permanent folds has been a matter of considerable speculation. It is evident that they increase the extent of the mucous surface to at least twice or thrice what it would be in a simple hollow cylinder of equal size. It is equally obvious, that their transverse position is peculiarly calculated to render this enlarged surface an effective one. For they are at right angles to the direction of peristalsis, and therefore to the general course of the intestinal contents. Such an arrangement of the mucous membrane, taken in connection with the great mobility of these folds, must not only insure a thorough admixture of the various constituents of the chyme, but, by delaying its direct passage onwards, bring every portion of it into contact with the greatest possible extent of the active intestinal surface.

Intestinal tubes. — The structure of the remaining constituents of the intestinal mucous membrane can only be seen distinctly by the aid of the microscope. Amongst these minute organs, the *intestinal tubes* — or, as they are commonly called, the *follicles of Lieberkuehn* — are the first to demand our notice. For, with slight modifications, they occupy the whole of the small and large intestine. An allusion has already been made to the fact that, in many animals, they appear to usurp a portion of the gastric cavity. While the importance which this wide distribution would imply, is confirmed by their immense number; which is such that we may estimate their aggregate surface as from ten to fifteen times that of the cylinder of intestine into which they open.

Each tube may be described as a hollow cylinder, having a length which is about five times its width, and ending below in a rounded

Fig. 256.



Intestinal tubes from the jejunum, as seen in a vertica section. (*Magnified* 80 *diameters.*)

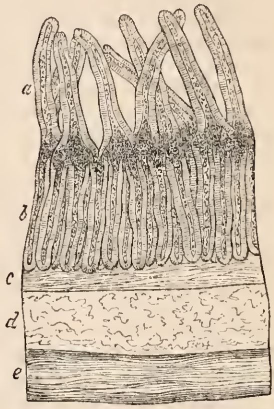
a, Limitary or basement membrane; *b*, nuclei of the columnar cells which line its interior; *c*, calibre or cavity of the tube; *d*, mouths of the tubes opening into the general cavity of the intestine; *e*, blind extremities of the tubes, corresponding to the submucous areolar tissue.

blind extremity. Its average diameter is about $\frac{1}{360}$th of an inch, except at its orifice, where it is somewhat wider. The lower part of the tube is often slightly enlarged: and rarely it appears to bifurcate. But while it is doubtful whether these appearances can be depended upon*, it is certain that they are not sufficiently marked or frequent to alter the above general description.†

This cylindrical tube is composed of basement membrane and epithelium. The former constituent needs no special description. The latter is a single layer of short columnar cells. It clothes the whole interior surface of the tubes; and becomes continuous, at their upper extremities, with the epithelium covering the villi, the constituent cells of which generally appear to be somewhat longer in shape. The cylindrical cavity bounded by these cells has a diameter which amounts to about one-fourth the width of the entire tube.

The arrangement of these tubes so precisely recalls that of the gastric glands into which their structure appears sometimes to merge, as scarcely to require any separate description. Like these, they are placed vertically side by side, in a sparing quantity of dense fibrous matrix; and are imbedded by their lower extremities in a layer of a similar appearance. The latter contain much unstriped muscle, the characters of which can be seen

Fig. 257.



Vertical and longitudinal section of the small intestine in the lower part of the jejunum, showing the general arrangement of its coats. (*Magnified* 50 *diameters.*)

a, villi; *b*, intestinal tubes; *c*, submucous areolar tissue; *d*, circular fibres of the muscular coat; *e*, longitudinal fibres, external to these, covered by peritoneum.

even more distinctly than in the analogous gastric structure. The aggregate mass of these vertical tubes forms the great bulk of the mucous membrane. So that a vertical section of this tunic exposes a dense pallisade of tubes, the depth of which corresponds to the thickness of the membrane: while a transverse one shows that the interstices of the cylinders are only occupied by a scanty matrix enclosing numerous vessels.

The chief interruption to their presence is caused by the racemose glands, villi, and follicles, which will shortly be described. The ducts of the first of these three structures merely occupy a certain portion of space which would otherwise be taken up by follicles. But the two latter encroach upon the surface of the mucous membrane much more considerably. And since it is only between the villi that we find the intestinal tubes, so the number of such tubes which occupy the intervals of these processes must necessarily correspond to the thickness with which the latter are strewed over the surface. Over the more projecting parts of the follicles, the tubes are also absent; in a circular space which is surrounded by a ring of apertures. The latter belong to the inflected upper extremities of

* See foot-note to p. 321.

† A more valid exception to the above statement may be found in the upper part of the duodenum of some of the domestic Mammalia; in whom many of these tubes divide, a little below the surface, into three or four smaller ones. This condition may be regarded as a transition from the structure of either the pyloric tubes, or the clustered glands of Brunn, to that of the ordinary intestinal tube. From the appearances offered by the cylindrical epithelium that lines their interior, the first of these conjectures may be regarded as the more probable of the two.

those tubes which immediately encircle each follicle.

When fresh, these tubes always exhibit the structure just described; their only contents being a clear, structureless, homogeneous fluid. But from their minute size, it is obvious that this fluid can never be obtained from their interior in sufficient quantity for any trustworthy analysis. While unless the secerning process were extremely rapid, even the secretion poured forth into the tube would often be mixed with those coarsely filtered contents of the intestine which can enter its upper orifice from the general cavity of the alimentary canal.

And as regards all fluids found in the general cavity of the intestine, we ought never to forget that to procure them in a state of absolute purity is impossible. Under normal circumstances, the fluid present in any part of the bowel can only be regarded as a complex mixture of several ingredients, all of which are probably themselves undergoing a continual metamorphosis. Could we deduct from the contents of the intestine all chyme, bile, and pancreatic secretion, the residue would be strictly an *intestinal juice*. And by far the larger quantity of such a juice would be composed of the secretion of the intestinal tubes. Now we shall hereafter find that analogy supplies us with some plausible conjectures respecting the fluid secreted by the duodenal glands. While the closed follicles which abut on the cavity of the bowel can scarcely furnish sufficient fluid seriously to affect the composition of any mixture which it may contain. Hence whatever the share taken by the villi, the secretory office of these tubes might apparently be to some extent determined from an examination into the chemical and physiological properties of even such an impure or mixed intestinal juice.

The reader will, however, hardly be surprised when he is informed, that these conditions have never yet been fulfilled; and hence, that a satisfactory account of this interesting fluid remains at present impossible. But he must not therefore think the above allusions superfluous. For it is only by a reference to these conditions of experiment, that we can judge how far we ought to accept the statements made by various recent observers respecting this fluid.

Thus Frerichs * obtained intestinal juice from fasting cats and dogs, in whom a few inches of intestine had been emptied, and tied at both ends, about five hours before they were killed. Lehmann † procured it from a fistula of the small intestine, which had followed an operation for hernia in the human subject; and in which another fistula, higher up, gave passage to the ordinary mixed contents of this part of the alimentary canal. Zander ‡ instituted fistulæ in animals. And, finally, Bidder § and Schmidt, who adopted Frerichs' method without obtaining one drop of intestinal juice, carefully compared the mixture withdrawn from simple fistulæ, with a very small quantity of a purer fluid which was yielded by dogs in whom the pancreatic and biliary ducts had been tied, and the gall bladder made to discharge its contents externally.

According to all these observers, the intestinal juice is a transparent, viscid, and strongly alkaline fluid. It contains nuclei, and round or columnar nucleated cells;—an abortive cell-growth, the admixture of which does not substantially affect the structureless character of the secretion. Of its composition and reactions we can only say, that it appears to contain mucus and the ordinary salts; which together form a solid residuum, that amounts to about 2 per cent. of the whole quantity of fluid.*

As regards the physiological properties of the intestinal juice, it has the power of converting starch into grape sugar. But however obvious the usefulness of this capacity, it is possessed in an equal degree by so many other animal substances, that it can hardly be regarded as the specific purpose or function of this secretion.†

But the recent observations of Zander, together with those of Bidder and Schmidt, claim for this secretion a much more important office:—an office which would entitle the whole of the small intestine to that appellation of a "*ventriculus succenturiatus*," which was formerly bestowed on the duodenum. These observers agree in the statement, that the intestinal juice dissolves protein-compounds, both in and out of the body. And from the careful quantitative researches of Bidder and Schmidt, it would follow, not only that its solvent powers upon these substances are from three to four times greater than those of the gastric juice itself, but that in the Dog, about half the daily albumen of a flesh diet is habitually left untouched by the stomach, to undergo solution in the intestine by the secretion.

Against such a conclusion I would suggest the following arguments, which together induce me to think that this doctrine ought not at present to be accepted. That a large organ like the stomach, with a definite and complicated structure, should so incompletely discharge its single chemical function, is a paradox which alone involves a great improbability. This suspicion becomes still stronger when we consider that, under normal circumstances, gastric juice is always conveyed from the stomach into the intestine during the process of gastric digestion; while it is evident that none of the experiments by these observers quite exclude the possibility of such a transit. Nay more, if we suppose—what is surely not

* *Op. cit.* p. 850.
† *Op. cit.* vol. ii. p. 112.
‡ Koelliker, *Op. cit.*
§ Lehmann, *Loc. cit.* and Bd. iii. s. 335.

* Bidder and Schmidt observed a much larger quantity in the mixed fluid; but point out that the fixed contents would be raised by the addition of the more concentrated secretions of the liver and pancreas. Hence I prefer quoting the estimate deduced by Lehmann from what was probably a purer fluid.

† Compare the remarks on the pancreatic fluid, in a subsequent part of this article.

impossible — that the juice carried onwards into the intestine is there concentrated by the partial absorption of its watery part, some of the strange quantitative results obtained by Bidder and Schmidt cease to be altogether inexplicable. It may indeed be urged, that the alkaline character observed in the intestinal juice sufficiently proves that its digestive properties are not derived from the stomach. But although the addition of a caustic alkali destroys the efficiency of gastric juice, still such a process seems very different from that absorption of acid, or that gradual admixture of a dilute alkaline solution, by which a similar reaction would probably be communicated in the living intestine. And, finally, is it like the ordinary economy of Nature, that an elaborate secretion should pass the pylorus, to be at once annihilated, and then replaced by a second and equally complex antagonist juice ? On such a supposition, indeed, there are many animals in whom almost all the gastric juice would be wasted. For example, there is great reason to suppose that the sojourn of food in the Horse's stomach is so brief, that anything like the stomach digestion of Carnivora is impossible. But are we therefore entitled to assert that this organ is utterly useless?

Such considerations appear to render it more probable, that the gastric juice may retain its digestive efficacy after passing through the pylorus ; and that the presence of this secretion in the small intestine sufficiently explains the solvent powers of the juice which is found in this situation.

But we are not left to such arguments alone to disprove the solvent powers ascribed to the intestinal juice by the above observers. They receive a still more direct contradiction from the experiments made by Frerichs* and by Lehmann.† These authorities concur to state, that neither in nor out of the body can it dissolve the protein compounds. And Lehmann's case may be regarded as affording much more than an ordinary negative result ; since in it, all communication between the stomach and the fistulous aperture made use of, seems to have been excluded.

Finally, we may recall to the reader that close parallel which was observed in the action of the gastric juice and the infusion of stomach ;—how, allowing for dilution and impurity, we found the latter behaving just like the former. Now, in striking contrast to this significant fact, numerous observers ‡ agree in representing the infusion of intestine as utterly incapable of that solvent action attributed by Bidder and Zander to its secretion. Indeed, Koelliker and Goll have found the capacity of digesting protein-compounds so intimately connected with the structure of the proper gastric tubes, as to be almost lost in the pyloric extremity of the Dog's stomach ; where these begin to assume the characters of intestinal tubes by losing their oval gastric cells.

Hence all these circumstances throw great doubt on the alleged solvent powers of the intestinal juice ; and render it impossible for us at present to decide what is the exact digestive office which it fulfils. And we are almost as ignorant of its quantity as of its quality. But it is probably secreted by the small intestine in much greater amount than by the large. According to Bidder and Schmidt, it is poured out most freely about five or six hours after a meal. And drinking soon increases its amount, without causing any converse diminution of its concentration. Its strongly alkaline reaction may be conjectured to have some relation to that large quantity of acid, which is apparently withdrawn from the chloride of sodium contained in the blood of the stomach, in order to furnish the gastric juice. Indeed, a liberation of soda or some other alkaline base, appears almost implied in that of the hydrochloric acid. But hitherto no exact analysis has informed us to what particular substance the alkaline character of the intestinal juice is immediately due. And it is only after a careful comparison of the composition and quantity of this secretion with those of the less alkaline bile and pancreatic fluid that we should be entitled to conjecture, how far the neutralization* of the acid peptone constitutes a special function of the intestinal juice. Still, from the great extent of secreting surface which yields this juice, we can hardly doubt, that it takes a large share in this neutralizing process, which was formerly attributed chiefly to the bile. It probably thus forms part of that cycle of alternate decomposition and recomposition, which appears to be undergone by the chloride of sodium.

The vascular arrangements by which these intestinal tubes are supplied with blood, so closely resemble those of the stomach-tubes, as to render any special description of them superfluous. Like the tubes themselves, the vessels are chiefly concerned with secretion. But while we are left in doubt as to the precise degree or kind of that absorptive function which the vessels of these tubes possess, in common with those of all such mucous surfaces, we are perhaps justified in attributing a special capacity of absorption to the plexus of large capillaries, which here, as in the former organ, lies immediately beneath the epithelium, around their open extremities. The loops of this superficial plexus are generally more simple than in the stomach. They encircle the mouth of each tube with what is often only a single ring of capillary (*b fig.* 258.) ; except in the neighbourhood of the solitary or agminate follicles, where they resemble the analogous gastric vessels in forming more complex meshes (*a fig.* 20.) They communicate very freely with the capil-

* *Loc. cit.*

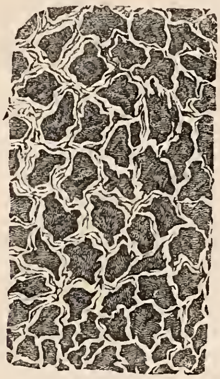
† *Loc. cit.*

‡ Koelliker, Valentin, Todd and Bowman, and others.

* It is impossible to state whether this neutralization of the gastric acid takes place during the sojourn of the gastric juice in the intestine, or after its absorption into the capillary veins around the canal.

laries of the neighbouring villi. And the venous radicles of these latter processes usually unite with the branches formed by their con-

Fig. 258.



Capillaries occupying the surface of the mucous membrane of the small intestine; as seen on examining an injected specimen by reflected light, with a magnifying power of about 50 *diameters.*

a, b, capillaries around the orifices of the intestinal tubes. At *a* their meshes are more numerous and complex than at *b,* where they are almost reduced to single capillaries; *c,* calibre or cavity of the intestinal tube.

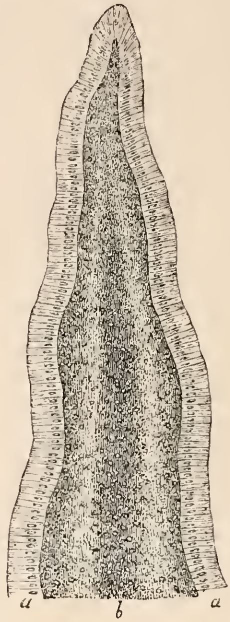
flux in a small vein; that sinks vertically through the mucous membrane, to join the sub-mucous plexus which gives origin to the portal vein.

Villi.— The interior of almost all the small intestine presents to the naked eye a texture very like that of velvet. For it is soft and shaggy: yields readily to pressure: and, on close examination, is evidently composed of innumerable short filaments, which are placed more or less vertically to the general inner surface of the tube. These filaments, — the dense arrangement of which on a common surface causes this general velvety appearance,— are thence usually named *villi.* Their form, and their situation, or office, might also be denoted by the name of *intestinal* or *chyliferous papillæ.*

We have seen that, in the stomach, the confluent ridges intervening between the tubes are here and there raised into slight projections. These are rendered more prominent by artificial injection of the subjacent vessels, or even by that afflux of blood which ordinarily attends the digestive act. In the pyloric extremity of the organ, these projections become more distinct. And just at its termination, some of them often assume the form of bluntly triangular and flattened folds.

In the upper part of the duodenum, the villi begin; by processes which somewhat resemble the gastric elevations just alluded to, and occupy an analogous situation with respect to the intestinal tubes. At first, they may be described as flattened folds, the outline of which is a very obtuse triangle, that has a broad base about four or five times its height ($\frac{1}{100}$th of an inch). In the lower part of the duodenum, this rudimentary form for the most part disappears; and the villi, which are still more or less flattened, have about twice the length, and half the width, of those present in the upper part. But it is in the upper part of the jejunum that they attain their greatest number; being placed so closely together that their interstices scarcely

Fig. 259.



Villus from the upper part of the jejunum, as seen in the fasting state. Magnified 140 *diameters.*

a, epithelium of the villus; *b,* parenchyma or substance of the same.

equal their own bulk. Here they also acquire their maximum length, which ranges from about $\frac{1}{30}$th to $\frac{1}{20}$th, or even $\frac{1}{15}$th or $\frac{1}{12}$th of an inch. Their form, however, is still that of a flattened cone (compare *fig.* 259. and *fig.* 257. p. 347.); —the breadth of the base of which is about $\frac{1}{8}$th, and the depth about $\frac{1}{10}$th, its height. In the remainder of the intestine, the length of the villi gradually recedes to that which they possess in the lower part of the duodenum; while their number also diminishes to a somewhat smaller extent. Throughout all this extent, the shapes and sizes of contiguous villi often present great varieties. But as a rule, the lower we descend in the examination of the intestine, the greater is the number of cylindrical forms we meet with. While towards the extremity of the ileum, the gradual diminution of their size renders many of them scarcely more than $\frac{1}{250}$th of an inch in diameter.

The villi cover the whole surface of the mucous membrane of the small intestine, including its valvulæ conniventes; and they extend to the free margin of the valve which marks the commencement of the cæcum and colon. The only exception to their presence occurs in the agminate follicles, or "Peyer's patches." Here they are absent over the several follicles which together form each patch; and become short, (*a*, *fig*. 272, p. 358.) blunt, irregular, or even confluent, where they occupy their interstices.

We have seen that each of the valvulæ conniventes is a doubled fold of membrane, separated by a layer of areolar tissue. While the minute intestinal tube may almost be regarded as a mere membranous lamina, which is involuted so as to surround a cylindrical cavity, and is packed in a sparing fibrous investment. But the villus constitutes, as it were, a solid process of the mucous membrane. In accordance with this structure, it consists of an epithelium, a basement membrane, a stroma or basis of fibrous tissue, unstriped muscle, and numerous blood-vessels. And in addition to these constituents, which may be found under various modifications throughout the whole intestinal mucous membrane, the interior of each villus encloses one or more branches of the lacteal vessels which contain the chyle.

The *epithelium* of the villi (*a*, *fig*. 259. and *a*, *figs*. 264, 265, 266.) consists of a single layer of cylindrical cells, which, — as regards size, shape, and general appearance, — closely resemble those seen on the ridges between the tubes of the stomach. They are, however, even more delicate in their structure, as well as more conical in their shape. And their contents are, even during fasting, somewhat darker and more granular. The nucleus, which occupies the same situation in both these varieties of cylindrical epithelium, contains a single bright spot, or nucleolus: in rare instances, this appears to be double.

The *basement-membrane* (at *b*, *fig*. 260.) does not require any special mention. As in the gastric ridges, it is very closely attached to the subjacent structures, especially to the vessels. But its continuity with the similar structure forming the intestinal tubes sufficiently indicates that it is really a distinct membrane. And it is often demonstrated to be such by the action of water; which, after transuding it from the outer surface, raises the membrane, in the shape of a delicate transparent bulla, from the general mass of the villus beneath.

The *blood-vessels* of the villi are extremely numerous.

Small arteries, (*a a*, *fig*. 260.) of about $\frac{1}{1000}$th of an inch in diameter, pass between the intestinal tubes. The base of each villus receives one, two, or more of these, according to its size. They now pass upwards in the substance of the process, at some distance from its surface; and rapidly diminish by giving off numerous capillaries, into which their own trunks entirely merge at about the middle of the height of the villus.

The ultimate capillaries themselves (*c c*, *fig*. 260.) are, on an average, about $\frac{1}{3}$rd of the above diameter. They constitute a net-work, which lies directly under the basement membrane; and covers the whole villus so thickly, as to give it a vivid red colour in injected specimens. The shape and complexity of this network is liable to great variety; but is usually such, that the length of its meshes is five or six times their width. The capillaries are distinguished by their being apt to exhibit a wavy and tortuous course (*d*, *fig*. 260.) which often causes their real length greatly to exceed that of the villus itself. This character is especially marked at the

Fig. 260.

Vessels of two villi, injected. Magnified 100 *diameters.*

a a, arteries entering the basis of each villus near its centre; *v v*, veins seen in the same situation; *c*, capillaries lying immediately beneath the limitary membrane; *d*, tortuous capillaries occupying the free extremity of one villus; *b*, limitary or basement membrane of the villus, denuded of its epithelium.

free extremity of the villus:—to the contraction of the muscular layer of which it would appear to be chiefly, though not wholly, due.

The veins (*v v*, *fig.* 260.) come off from this network by the gradual union of capillaries in the upper half of the villus, so as to form two or more venous trunks. These are usually about double the width of the corresponding arteries: they run at a distance from them; and often lie rather nearer to the surface of the villus. Below, these trunks become confluent in the single vein of the process; which, passing vertically downwards, terminates by joining one of the numerous veins belonging to the venous plexus around the orifices of the intestinal tubes. And this latter network also joins that of the villus by such numerous communications, that the two might almost be regarded as merging into each other.

The substance which forms the groundwork or *basis* of the villus resembles, to some extent, that of the gastric mucous membrane; — the morphological constituents of which we have already seen to be indistinct, except at the bottoms of the tubes. It rarely presents any definite structure. Sometimes, however, it is faintly striated. And occasionally this appearance is so marked, as to approach a fibrous character. In this respect, it resembles the papillæ of the skin and tongue; — and, especially, those secondary projections which stud the fungiform papillæ of the latter organ, the basis of which contains no yellow elastic fibres, but is almost homogeneous, and often indistinctly granular.

Mixed with this indistinctly fibrous tissue are numerous delicate cytoblasts or nuclei (*b*, *figs.* 259, 261, 262, 263.). The larger of these attain the size of coloured blood-corpuscles; while the small merge into granules by increasing minuteness. The exact relation of these to the basis of the villus is unknown. Their general effect is to communicate to the whole villus a more or less mottled and granular aspect. This appearance (which we shall find is increased during the period of intestinal digestion) often obscures, not only the vague fibrillation just alluded to, but the whole of the structures which lie beneath the basement membrane.

As regards the *lacteals* of the villi, few anatomical details have been more disputed than those which relate to the commencement of the chyliferous absorbents within the substance of these processes. The progress of microscopical research has, however, reduced the controversy within very narrow limits; and promises at no distant date, to end it by a final decision. At present, almost all trustworthy observers agree in the statement, that each villus receives by its base a single (perhaps sometimes a double) branch of the lacteal system. It is only as to the further course of this vessel that opinions differ. Many affirm it to be continued up the villus as a single tube, which ends near its apex by a blind and often somewhat dilated extremity. Some authorities modify this view for the broader villi, by stating the canal to be double—either as a single loop, or as a bifid and somewhat tortuous tube. While others find that the central and simple lacteal canal ends by branching into a network of more or less complex character, like that of the capillaries.

The first of these statements will at any rate apply to many of the villi. Numerous observers have verified its accuracy for the human subject. And it is not difficult to obtain distinct evidence of its truth in some other Mammalia. Amongst these the sucking Rabbit and Calf are especially suitable for examination. If proper care be taken to examine the chyliferous villi of these animals instantly after death, with the aid of suitable fluids, we may easily convince ourselves of the presence of a single large lacteal tube, with distinct walls, like that represented in the annexed figure (*fig.* 261.). Such

Fig. 261.

Two villi, denuded of epithelium, with the lacteal vessel in their interior. From the Calf. Magnified 350 *diameters.* (*After Koelliker.*)

a, limitary membrane of the villus; *b*, matrix or basis of the same; *c*, dilated blind extremity of the central lacteal; *d*, trunk of the same.

single lacteals are generally very large, having a diameter which often amounts to about one-third or one-fourth that of the villus itself; and exhibit a dilated blind extremity, (*c*, *fig.* 261.) which nearly doubles their width. In man, according to Frerichs *, they are scarcely more than one-half or two-thirds of this size.

But it remains to be considered whether this

* *Op. cit.* p. 751.

statement excludes the possibility of a network, such as has been affirmed to exist by Krause and others. Koelliker, in whose admirable work * the reader will find a copious analysis of the latest observations on this subject, sums them all up very impartially by acknowledging, that, although he has never been able to see a trace of such ramifications, still he cannot venture altogether to deny their existence. On the contrary, he thinks it possible that the above simple mode of commencement,—which certainly holds good for the cylindrical villi,—may be exchanged, in the larger of these processes, for one involving the presence of a greater number of lacteal canals, or the absence of such blind extremities.

But in conceding this much, Koelliker points out—what Valentin † seems previously to have suspected,—the facility with which a striated arrangement of the dark fatty molecules within the chyliferous villus may be mistaken for lacteal vessels. Nay more, even the chyle of the central canal sometimes separates by coagulation into striæ, which closely imitate a branched network. We may add, that, in the various observations which have been made on executed criminals, the possibility of error has probably been increased by the distended state of the vascular and lacteal canals contained within the delicate structure of the villus.

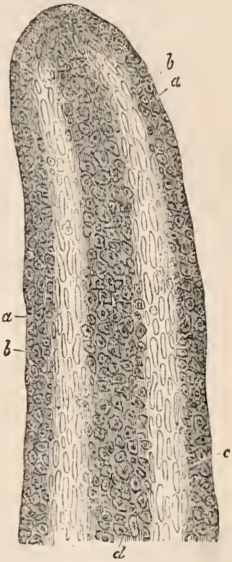
Whatever be the case as regards these conjectures, it seems to me that the large simple tube, and the minute network, are far too unlike to be regarded as mere degrees of development of the same structure in different villi. In like manner, the simple loop of lacteal seen by Henle just beneath the basement membrane is suspicious, not only from its situation, but also from a fact noticed by Valentin and Remak,—that the central canal sometimes coexists with it. And when we add to the foregoing remarks, that the majority of observers have been unable to see any such ramifications, it will seem difficult to avoid concluding, that each villus probably contains a single large lacteal, which occupies its centre, and ends by a blind extremity.

The *muscular* constituent of the villus was first discovered by Bruecke, and has since been verified by Koelliker in many Birds and Mammals. Its shape is that of a thin hollow cone, which closely imitates the form of the villus enclosing it. Hence, from whatever side it is examined, it may be seen as a double longitudinal layer; which is placed immediately around both sides of the central lacteal; and lies so deeply within the villus, as to be beneath its vessels, as well as much of its granular basis. It is more distinct in the lower part of the villus, and in the larger flat specimens; but is easily obscured by oil globules, nuclei, or pigment. The nuclei of its fibre cells are best seen on the addition of dilute acetic or nitric acid, when they assume their ordinary characteristic appearance.

* *Op. cit.* p. 160. et seq.
† *Op. cit.* p. 684.

The action of this contractile apparatus during life is at present unknown. Derived, as it no doubt is, from that general expanse of

Fig. 262.



Villus denuded of epithelium, treated with acetic acid. From a young kitten. Magnified 350 *diameters.* (*After Koelliker.*)

a, outline of the villus; *b*, nuclei beneath this; *c*, nuclei of the unstriped muscle; *d*, roundish nuclei in the centre of the villus.

unstriped muscular fibre which pervades the whole mucous membrane of the alimentary canal, one can hardly avoid ascribing to it a function which is more or less similar,—if not indeed co-ordinate,—with that of the general stratum. That this function is in some respects related to the static or passive mechanical circumstances of the mucous membrane, has already been conjectured (p. 325.) in speaking of the stomach. And the little we know of the ordinary action of the analogous unstriped element in the skin, rather confirms than contradicts such a supposition. But its peculiar position with respect to the end of the lacteal trunk in the centre of the vi lus,—to which it forms a kind of muscular and contractile envelope—has given rise to the suspicion, that it effects the propulsion of the chyle contained in this canal.

How far such a process really obtains must be determined by future research, which ought especially to notice the precise connection of this muscular stratum with that of the mucous membrane generally. In the meantime, we may notice that, as Koelliker justly remarks, an active propulsion by these longitudinal fibres would imply their alternate contraction and relaxation.* But, assuming

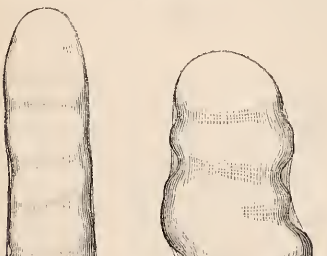
* He also adverts to their apparent want of nerves, and to the essential independence of organic muscle of all but mechanical irritations. However

this to occur, it is evident that such a remittent contraction would not destroy the claims of the absorptive act itself to be considered the chief force which propels the chyle. For in any case, the muscular apparatus would but limit and remove that distention of the lacteal which absorption had previously effected. It would thus, as it were, merely regulate and transfer the mechanical force of the latter act; so as to modify it, either constantly, or at definite intervals of time.

Some observers have attempted to verify the action of this delicate muscular apparatus during life. Gruby and Delafond first instituted such observations on a variety of domestic animals; and they have since been repeated by Bruecke and Koelliker. All of these authorities agree in remarking an alternate shortening and elongation of the villus: — a change of form which is so rapid and marked, that there need be little hesitation in attributing it to a corresponding contraction and relaxation of these unstriped fibres. But the phenomena seen in the course of such vivisections cannot be safely accepted as those of the healthy animal in its natural state.*

Such a caution is still more applicable to those contractions by which the villi share in that irregular movement of the intestine already described as a kind of *rigor mortis*. On exposing the villi of an animal soon after death, they gradually become shorter and

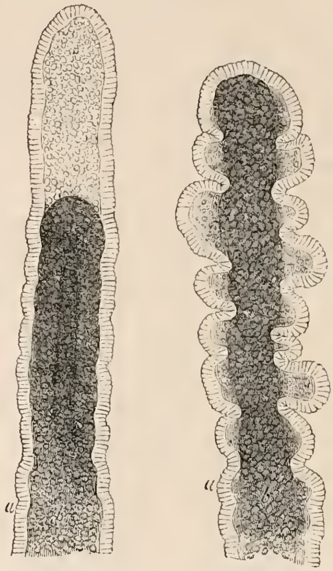
Fig. 263.



Villi contracted and shortened so as to offer circular or transverse wrinkles. From the small intestine of the dog shortly after death. Magnified 100 diameters; and examined by reflected light.

wider; at the same time that their surface is generally thrown into circular transverse wrinkles or folds. A more minute examination shows that these folds consist of epithelium, which has separated from the basement membrane at the points that correspond to the greatest projection between the contiguous wrinkles (*fig.* 264, 2.) A closer adhesion of

Fig. 264.



1. 2.

Similar villi as seen by transmitted light. The villus marked 1, *has been partially withdrawn by contraction from its investing epithelium, which is thus left entire like the finger of a glove.*

a, epithelium of the villus; *b*, granular matrix or substance of the same.

those columnar cells which occupy the free extremity of the villus, frequently causes this part to be defined, as a shallow funnel, by the neighbouring separated cells. While in other instances, a variable length of the whole villus withdraws from its cellular investment with such uniformity, as to leave the extremity of the latter empty, smooth, and uninjured (*fig.* 264, 1.), like the finger of a glove. Frequently, however, some of the epithelial cells are detached.

It is obvious that all these appearances are referrible to a contraction of the unstriped fibres within the villus, withdrawing the substance of the latter from its epithelial investment. The movements which often accompany these changes resemble those above mentioned as beheld during life; and consist of shortening or elongation, to which are sometimes added lateral displacements. The date of their occurrence is limited to the period

general this view of the action of unstriped fibre, I must confess myself very reluctant to accept it on its present evidence.

* For,—to say nothing of the pain, the irritation, and the exposure, which are involved in such an opening into the intestine as is necessary to allow a proper inspection of the villi,—Gruby and Delafond remark, that their surface becomes wrinkled and pale at the time of their contraction. Such circumstances imply so much disturbance of these soft structures, as to throw great suspicion upon any view which would interpret them as part of a normal process.

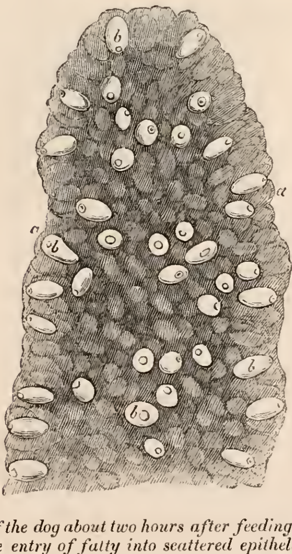
which immediately succeeds death. And their duration is rarely protracted beyond a few minutes.

Changes in the villi during digestion. — During the act of digestion, the villi undergo certain noticeable alterations. At this period, they receive an increased afflux of blood; and become both larger and softer. They acquire a greater opacity; so as to appear whiter by reflected, and darker by transmitted, light. The nuclei and cells which occupy their interior are greatly increased in number and distinctness. And, finally, after the ingestion of food containing the usual fatty ingredients, a portion of these may be found occupying the interior of the villi themselves.

The process by which fatty matter penetrates the villus to enter the lacteal in its centre, deserves our special attention, from the fact that it constitutes the origin of the chyle. At present we shall limit ourselves to a description of the appearances actually observed, in connection with the mucous membrane of the alimentary canal.

The first step towards the absorption of the fatty matter, consists in its entry into the epithelium which invests the exterior of the villus. Each columnar cell of this covering is gradually filled by a large oil globule; which occupies the whole of its cavity, with the exception of that small portion devoted to its nucleus. This change first implicates a few scattered epithelia; and, by rendering them

Fig. 265.



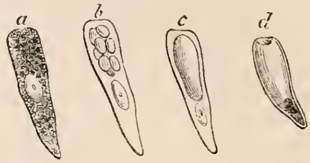
Villus of the dog about two hours after feeding: showing the entry of fatty into scattered epithelia on its surface. Magnified about 400 *diameters.*

a, a, outline of the villus formed by epithelia with their ordinary contents; *b, b,* epithelia rendered bright and refractile by their fatty contents.

more refractile, often causes various parts of the surface of the villus to offer a curious contrast of bright spots (*b*, *fig.* 265.) and darker intervals.* Gradually, however, all the cells become similarly affected; so that the entire villus assumes the altered appearance just alluded to.

The next step towards the absorption of the fatty matter consists in the minute subdivision of the single oil globule (*c*, *fig.* 266.) which occupies the epithelial cell. The way in which this process occurs is unknown:

Fig. 266.



Isolated epithelial cells from a villus, as seen during the absorption of fat into the lacteals. (*Altered from Koelliker.*) *Magnified* 350 *diameters.*

a, columnar epithelial cell, occupied by fatty molecules; *b,* similar cell, containing several small oil-drops; *c,* similar cell, enclosing a single oil-drop; *d,* similar cell completely filled by a larger oil-drop. The upper or free end of the cell (at *d*) is concave.

but the result of the change is to give the columnar cell a darkly granular appearance (*a*, *fig* 266.), in which we may often distinguish separate, though minute, fatty molecules. These molecules are next found in the substance of the villus itself, though chiefly towards its surface and free extremity; — to the apex of which latter part they are often limited.† From the substance or matrix of the villus, the molecules of fat are then transferred to the lacteal trunk occupying its centre; which, in the most favourable instances, they define as a slender column of dark fatty granules.

How far the above process constitutes a mere act of physical imbibition, it is difficult at present to determine. But that it is so, at least in part, can scarcely be doubted. For the experiments of Matteucci ‡ (which are confirmed in all their essential particulars by Valentin §) prove that, when a dilute alkaline solution and a faintly alkaline fatty emulsion are separated from each other by an animal membrane, diffusion occurs between them. And the circumstances actually present in the intestine are even more favourable to such a transit than those which obtained in the experiments of these observers. The lymph and blood are sometimes more alkaline than the solution which they made use of. The degree in which the tenuity of the delicate cell-wall of the villus exceeds that of the

* These appearances, alluded to by Frerichs (*Op. cit.* p. 854.) and detailed by Koelliker (*Op. cit.* p. 167.), were noticed by me eight years ago in the human subject.

† The larger drops sometimes seen in this situation are, I believe, the result of accidental violence to the specimen.

‡ Leçons sur les Phénomènes, &c., pp. 104, 5.

§ *Op. cit.* vol. i. p. 379.

compound membrane forming the diffusive septum in their experiments, would proportionately favour the resulting transit of the separated fluids. And since the continuous movement of the chyle is probably aided by forces independent of any mere act of diffusion, the force of suction thus added must itself conditionate a more active transit than that which they witnessed in the inert endosmometer.

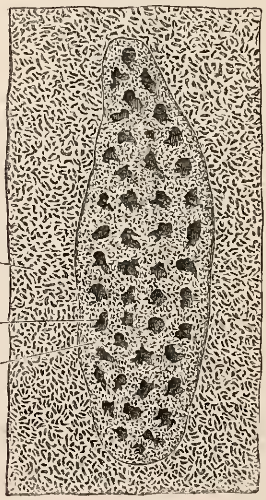
On the other hand, there are good reasons for regarding the reception of fatty matters as a much more complex phenomenon, and the result of what we may venture to call more vital processes. For the way in which ether and other solvents act upon the chyle appears to prove, that the fatty contents of its molecules are still oily; and not saponified, like such diffused fluids. And while the position of the capillary plexus, and the rapidity and quantity of its stream, render it probable that any merely diffusive action would disproportionately affect the blood—which by the way is often more alkaline than the chyle —a chemical and physical comparison of these two fluids would seem to show that the reverse is actually the case: that a larger quantity of fat is taken up by the lacteals than by the blood-vessels. This view is also confirmed by the results of violent inflammation *, or of great interference with the blood-vessels †: — changes, neither of which would probably have much direct effect on the physical action of an independent system of tubes, but which are nevertheless alleged entirely to prevent the formation of chyle. In any case, it would seem that there are strict limits to the quantity of fatty matter which can be absorbed. Hence when the amount of fat present in any particular region at all exceeds what its villi can take up, it is passed on to other portions of intestine; failing absorption by which, it is ultimately discharged unchanged in the fæces.

Intestinal Follicles.‡ — We pass on to the description of a class of structures which are essentially closed sacs; and which, represented in the stomach by the lenticular glands, pervade all the remainder of the intestinal canal under the two forms of *solitary* and *agminate follicles:* the latter being, as their name implies, essentially clusters of the former.

Agminate follicles. — Of the very numerous § names which have been bestowed upon these follicles, that above made use of seems preferable; since it best connotes both their structure and arrangement. There are generally about twenty clusters of these agminate follicles scattered throughout the small intestine. Their shape is commonly that of an oval, having a length about twice its width. They are situated on the free border of the bowel, or opposite to the attachment of its mesentery; and usually correspond to about the lower three-fifths of the small intestine, or to that part of it which is regarded as the ileum. Hence they have been looked upon as, in a certain sense, characteristic of this region. But they sometimes extend into the jejunum, being scattered sparingly throughout its lowest segments. And they may rarely be found even in the duodenum. In such cases, their entire number is usually about twice or thrice that of the average given above.

But amid all their variations of number, size, and extent, the agminate follicles seem to retain a certain predominant relation to the end of the ileum. For it is here that they are both largest and most numerous. And while in the remainder of the small intestine, their length is usually rather under than over an inch, nothing is more common than to find the immediate neighbourhood of the ilio-cæcal valve occupied by a single irregular cluster;— which has a length of two, three, or even four inches, and a width which carries it round $\frac{2}{3}$ds or $\frac{3}{4}$ths of the inner circumference of the intestinal tube.

Fig. 267.



Agminate follicles as seen by reflected light. Magnified 4 diameters. (After Koelliker.)

a, general mucous surface with villi; *b*, depressions leading to the several follicles; *c*, intervals between them, covered by small villi.

On examining the mucous membrane of the

* Frerichs, *Loc. cit.*

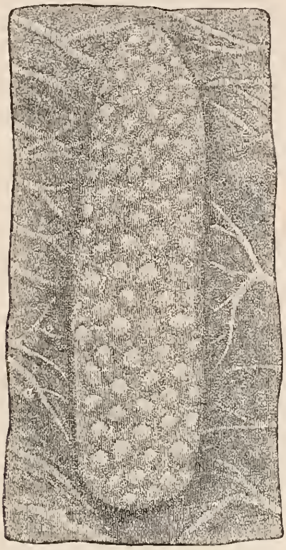
† Fenwick in "Lancet" for 1845, p. 64.

‡ The etymology of the word "*follicle*" quite permits its application to these closed sacs: to which indeed it seems desirable that we should restrict it, in speaking of the various constituents of the intestinal mucous membrane.

§ Until a more uniform nomenclature is adopted, it seems advisable to enumerate a few of these names. Such are the titles of *glandulæ Peyerianæ; agmina Peyeri; glandulæ aggregatæ; glandulæ agminatæ; vesicularum agmina; plexus intestinales; plaques gaufrées;* and finally, *Peyer's patches.* The latter uncouth designation is, perhaps, that most commonly made use of in this country. But as Peyer appears to have been anticipated by our countryman Grew in the discovery of these structures, there is the less need of clinging to one of those unmeaning surnames, which every practical teacher of anatomy will probably agree with the author in thinking very objectionable.

bowel by reflected light, at a place corresponding to a cluster of agminate follicles, we see that its surface (which is raised above the rest of the intestine, but has no very sharp line of demarcation from it) is occupied by a number of irregular shallow depressions (*b*, *fig.* 267.), at tolerably uniform distances from each other. But when inspected by transmitted light, these fossæ are replaced

Fig. 268.



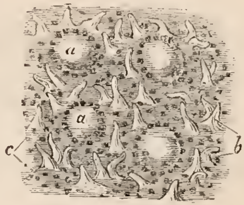
Agminate follicles as seen by transmitted light. Magnified about 5 diameters. (After Boehm.)

a, general mucous surface of the ileum; *b*, *b*, opaque grains corresponding to the several follicles.

by comparatively opaque grains (*b*, *b*, *fig.* 268.), of about the size of a millet seed; the aggregation of which renders the whole cluster very distinctly visible by this mode of examination. Finally, the cluster may often be recognised externally, from the bulging of the peritoneal coat which it causes in this situation. Indeed, its constituent follicles may sometimes be seen glimmering through the delicate muscular tunic.

Each such cluster is composed of a number of follicles, varying from twenty or thirty in the smaller, to at least one or two hundred in the larger, specimens. A careful examination of the mucous surface shows that the depressions just mentioned do not lead to any apertures, but are terminated by a smooth surface, the convexity of which somewhat diminishes their own depth. It is only at the margins, and in the intervals, of these fossæ, that we find the tubes and villi proper to the small intestine. And both of these latter structures are somewhat modified. Those tubes which immediately surround each depression have a circular or elliptical arrangement; so that their orifices generally form a ring of ten to twenty tubes in the fossa (around *a*, *fig.* 269.), and thus give rise to a very characteristic appearance.* In like manner, the villi in their immediate neighbourhood often appear to radiate outwards

Fig. 269.



Portion of a cluster of agminate follicles.

a, *a*, follicles encircled by apertures of the intestinal tubes in the form of a ring; *b*, short and obtuse villi, occupying the intervals of the follicles; *c*, apertures of intestinal tubes, opening irregularly in these intervals.

from a point corresponding to the centre of the fossa. And both they, and those more equidistant to the several follicles, are very different from the villi seen elsewhere:— being fewer (*b*, *fig.* 269; *a*, *fig.* 270.), shorter, of more irregular form, and often confluent at their bases.

To demonstrate the structure and arrangement of the several constituent follicles of the agminate clusters, requires great care, and very delicate manipulation. At the free surface of the mucous membrane, they are extremely difficult to isolate; both from their great tenuity, and their intimate union to the neighbouring tubes. Hence the best way of gaining access to them is from the outside of the intestine, where they may often be seen through the peritoneal and muscular coats.† The removal of these tunics brings them directly into view. To this method of examination must be added careful section in the vertical and horizontal planes.

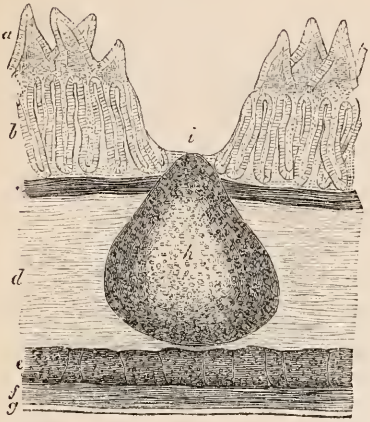
A proper combination of all these methods of investigation reveals the following facts.— Each follicle is a shut sac: having a roundish form, but a somewhat conical apex, which is directed towards the surface of the mucous membrane. Their diameter varies from 1 to 2 or 3·50ths of an inch. The base of each is in contact with the muscular coat (which is somewhat thinned in this situation); and is united to it by an areolar tissue that resembles the ordinary loose sub-mucous texture, in which the follicle is imbedded by the greater part of its bulk. The short apex of the follicle extends upwards between the lower extremities of the intestinal tubes: and, below their middle, it terminates in the immediate neighbourhood of the general mucous surface, which has already been

* This appearance is somewhat incompatible with that seen in a vertical section. Hence it is perhaps partially due to pressure or over-distention of the follicle.

† Especially after having been rendered opaque by soaking in dilute acids, which coagulate their contents.

described as depressed into a fossa in this situation. The thin stratum of tissue which

Fig. 270.



Plan of an agminate follicle, as seen by a vertical section. Magnified 40 *diameters.*

a, short and conical villi surrounding the follicle; *b*, intestinal tubes in the same situation; *c*, muscular stratum of the mucous membrane; *d*, submucous areolar tissue, in which the follicle is chiefly situated; *e*, circular layer of the muscular coat; *f*, longitudinal layer of the same; *g*, peritoneal coat; *h*, follicle enclosing nuclear contents; *i*, apex of the follicle projecting into the cavity of the bowel.

intervenes between the follicle and the interior of the bowel (at *i*, *fig.* 270.) is so delicate, that its exact anatomy is not easily verified by vertical sections. It appears, however, to consist of a very small quantity of indistinctly fibrous tissue; which encloses some capillaries, and is covered by the ordinary layer of columnar epithelium.

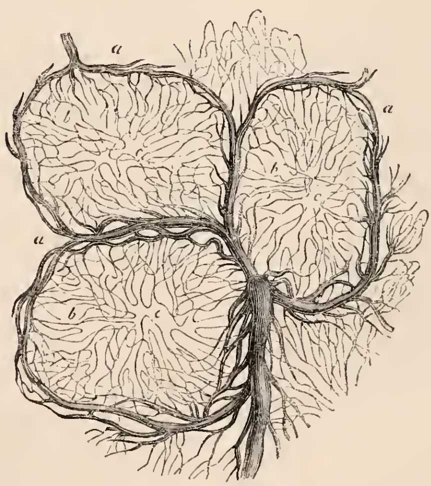
The frequent rupture of the follicle in this situation has led many to regard it as either possessing a permanent orifice here, or acquiring one by a kind of natural dehiscence. But later researches seem to show that this open state is quite exceptional and accidental; being due to disease, putrefaction, or mechanical violence. The author can at least express his own conviction that—as Boehm long ago stated,—the agminate follicles are closed sacs. This conclusion is much confirmed by the fact, that the follicles of some animals are altogether beneath the mucous membrane and the tubes, and quite distinct from both of them; so as to lie wholly in the sub-mucous areolar tissue.* While the vascular arrangements which we are about to describe seem equally incompatible with any theory of their normal dehiscence.

Each of these follicles essentially consists of a capsule, enclosing a number of delicate capillaries, the interstices of which are occupied by a cell-growth consisting of various forms.

The *capsule* is a structure which, though analogous to a basement membrane, differs from such a delicate homogeneous lamina, both in being much thicker, and in offering an indistinctly fibrous texture. Its smooth outer surface contains elastic fibres, and is attached by loose areolar tissue to the surrounding sub-mucous structures.

The *vessels* of the follicle offer a very peculiar arrangement. The small arteries in the sub-mucous areolar tissue give off branches that ramify amongst the several follicles of each "patch;" and thus form a network of

Fig. 271.



Vessels of the three agminate follicles of the Rabbit; as seen by a horizontal section, at about the middle of their height. (*After Koelliker; from an injection by Frei.*)

a, a, minute vessels surrounding the capsule of the agminate follicles; *b, b, b,* delicate capillary loops *a,* penetrating their interior, and bending back from *c, c, c,* the centres of the follicles.

capillary arteries, chiefly occupying the horizontal plane. These vessels, which are in contact with the capsule of the follicle, break

* Compare Koelliker, *Op. cit.* pp. 153. 188.

up into numerous capillaries of about $\frac{1}{3000}$th of an inch in diameter. The latter surround the membranous wall of the follicle with an irregular plexus. But where they reach the middle of that part of it which projects into the interior of the intestine, they are curved back upon themselves ; so as to form long loops, that radiate from a central space quite uncovered by vessels. And this appearance, which was depicted long ago by Boehm, does but represent, at the surface of the follicle, what the more recent researches of Frei prove to be the vascular arrangement that pervades the whole of its interior. The injections of this anatomist show, that the capsule is not only surrounded by the network just mentioned, but is also penetrated by a number of minute capillaries. These, which are of a still smaller diameter than the former vessels, leave them at right angles, and reach nearly to the centre of the follicle, before looping back again to its exterior. And finally, some of the uppermost of them have been traced by Koelliker uniting to form the radicle of one or two veins of about $\frac{1}{1000}$th of an inch in diameter; which descend vertically through the follicle, without receiving any further branches from the neighbouring capillaries.

The remaining *contents* of the follicle form a soft pulpy mass. This is remarkably contrasted with the contents of the neighbouring lacteals, in the fact that it is always of a pale, semi-transparent, greyish colour ; while the latter are, during digestion, of a brilliant white. The application of reagents under the microscope shows this greyish pulp to be composed of a proteinous substance closely akin to albumen. The addition of water causes it to swell up, and effects its partial solution. And as regards its structure, the mass consists of a moderate quantity of fluid, mingled with a variety of cells. These, however different in their characters, may probably be all reduced to various forms of cell-growth, on the one hand; and various stages of the retrograde solution of blood-corpuscles, on the other. The latter process, though by no means uncommon, appears always due to an extravasation of a more or less accidental character. It is the cell-growth which constitutes the specific histological character of these albuminous contents of the follicle.

The cell-growth ranges from distinctly nucleated cells, of $\frac{1}{2000}$th of an inch in diameter, to cells of about one-half, and through these to nuclei of barely one-third, the above size. The latter, however, are of nearly the same bulk as those contained in the largest cells. Hence it would seem that the process of growth which these differences indicate, consists chiefly in the isolation and removal of the cell-wall, from its previously close apposition around the nucleus. In the Sheep, however, Koelliker has sometimes observed an endogenous multiplication of large cells, by a subdivision of their nuclei. And in other specimens from the same animal, he has noticed what is very possibly the opposite extreme of the cell-life : — the cavity of a large cell filled with large angular corpuscles. These corpuscles are sometimes nucleated; they have albuminous reactions; and they appear to be produced from the ordinary cells of the pulp. They ultimately disappear.

The *function* of the agminate follicles it is impossible to specify. Few organs in the body have been the subject of more numerous speculations: — speculations, the absurdity of most of which renders them unworthy of any serious mention. And hence, although what we know respecting the structure of these organs justifies (or rather requires) some attempt to indicate their physiological import, the mistakes of others may well teach us how much caution is requisite in making such conjectures. They are, at most, mere guesses at truth.

The contents of the follicle have just been stated to be composed of a cell-growth that lies in contact with a large vascular surface. Hence it is in the reaction of these innumerable minute agents on a copious and rich nutritional fluid exsuded from the blood, that we must look for the chief office of the follicle. The fact of various stages of cell-life being present simultaneously, appears to indicate, that the cells do not merely select certain materials, but more or less produce them; by a process which, directly or indirectly — by absolutely consuming their tissue, or otherwise — involves their own decay and death. So far, then, the agminate follicle, which closely resembles the vascular gland in its structure, might be conjectured akin to it in its function ; — that function being a choice from the nutritional fluid of certain of its constituents, which, after undergoing a metamorphosis, are subsequently returned into the general current of the blood.

But such a view omits to recognize some of the circumstances it ought to explain. And it especially neglects one which must be supposed of great importance : namely, the situation of the follicle ; or, in other words, its peculiar relation to the cavity of the intestine.

It is obvious that the position of the agminate follicle with respect to the intestinal canal will admit of a double interpretation. On the one hand, the materials on which its enclosed cells have to act, will probably be derived from the contents of the alimentary canal, as well as from the blood. And on the other hand, they may be ultimately excreted from the body through the intestine, as well as returned into that system of closed canals which the blood vessels compose.

The degree in which the intestine forms the channel of such an ingress and egress, must of course depend upon the directness and efficiency of the communication between its cavity and that of the follicle. Hence, where the two are in such close contiguity to each other as in the case of the agminate glands of the human subject, we may presume that an efficient transudation of this twofold nature really does obtain. But where, as in some of the follicles of the Calf, the cavity of the intestine is separated from that of these minute sacs by the intervention of a thick compound mucous membrane, it is difficult to avoid the conclusion; that a transit of their fluid contents, in either, direction can only obtain to a comparatively small amount.

In addition to these important relations between the agminate follicle on the one hand, and the vascular and intestinal cavities on the other, recent observations have shown that there is a third, which is perhaps quite as intimately connected with its function: — namely, the connection of the follicle with the commencement of the lacteal system. For the general analogy of the intestinal follicle to the vascular gland is far surpassed by that close structural resemblance which Koelliker has shown that it possesses to the follicles of the lymphatic glands. The latter, indeed, exhibit a remarkable similarity to the structure of the agminate follicles. Like them, they enclose vessels as well as cells, within the cavity formed by their limitary wall. Hitherto it has certainly been found impossible to verify the presence of lacteals within the agminate follicles; or to establish the existence of any direct communication between their cavities and that of the lacteal vessels themselves. But in spite of this, it seems certain, both that the lacteals occupy the patches in numbers quite disproportionate to the small and few villi here present; and that they possess the closest proximity with the contents of the follicles. Such a * conclusion must, I think, be drawn from Bruecke's researches; in which the cavity of the follicle soon became slightly coloured with reddened turpentine, which had been injected into the lacteals by compressing the distended intestine.

It remains, however, for future researches to determine how far this view is correct, and whether the agminate follicles do really partake of the nature and office of lymphatic glands. In any case, their very variable number, and their occasional absence, would seem to indicate, that (like the similar structures always present in the tonsils, and sometimes found in large numbers within the mucous membrane of the stomach) their function is either not very important; or — what is far more likely — can be more or less replaced by that of other kindred organs. And from the number and size of these follicles, we may perhaps conjecture, that their merely quantitative effect on the chemistry of the organism is not very great.

The little that is known of their changes in health and disease confirms what has just been stated respecting their relations to the vascular and lymphatic systems. Thus, during digestion, they become so swollen, as to project from the inner surface of the intestine: — a condition that may, perhaps, be due to increased absorption from the intestine, but is better ascribed to that energetic determination of blood to the whole of the intestinal structures which then takes place. During the violent drain of cholera the same tumid condition obtains: probably from a similar cause. And finally, the remarkable parallel between the disease of these follicles and that of the neighbouring mesenteric glands, which is seen both in phthisis and typhoid fever, is a strong additional argument for the reality of that analogy which physiology indicates to exist between the two structures.

Solitary follicles. — The *solitary follicles* are so completely what their name implies — isolated structures of the same kind as those which are aggregated to form the "patch" — that any further description of their minute anatomy would be quite superfluous. Indeed, those smaller patches which are formed by two or three follicles, may be almost regarded as a transition between the "solitary" and "agminate" arrangement. But these scattered solitary follicles are seldom or never surrounded by a definite circle of the apertures of intestinal tubes. And they often sustain villi of the usual size and shape. Their number is extremely variable. Sometimes they seem to be altogether absent. But a very careful examination will now and then show, that such a deficiency is one in appearance only; and is due to the very slight degree of distention which obtains in the follicles really present. Whether this explanation would always hold good is more doubtful: though the remarkable constancy with which these structures are found in most animals and in the human fœtus is, to say the least, a strong confirmation of its general truth. In other instances they are strewn thickly over the whole intestinal canal, from the œsophagus to the anus. Such an excessive development is perhaps strictly a morbid phenomenon. But it is also capable of explanation as a mere collective hypertrophy; — an overgrowth which results in an increased number of these minute organs, instead of an increased size of each individual follicle. Which of these two views is the more correct, will only be decided when we know more respecting their office.

They usually occupy the whole of the small and large intestine in considerable numbers. They are, however, more numerous in the latter of these two segments of the digestive tube. And here they also present a larger size, as well as what is generally a deeper situation in the sub-mucous areolar tissue. Hence the depression that indicates the follicle in the small intestine is exaggerated, in the large intestine, into a deep fossa; which, commencing by an aperture over each follicle, widens as it passes downwards between the opposed sides of a few contiguous intestinal tubes, to terminate, near their

* That direct communication between the agminate follicles and the lacteals, which Bruecke deduced from his observations, is, however, contradicted by the time at which the colour above mentioned appeared, and by its diminished intensity of hue: — as well as by the fact, that the agminate follicle never contains white chyle.

extremities, on the bulging surface of the follicle.

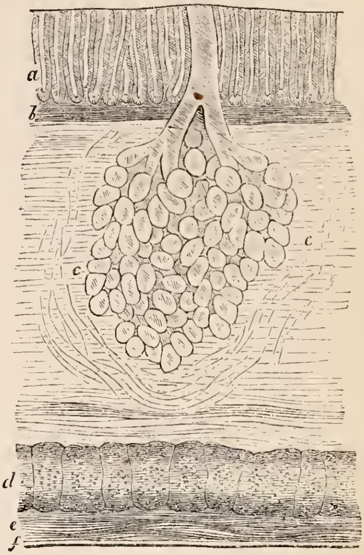
Racemose, or *Brunn's glands.* — The remaining constituent of the compound intestinal membrane is one which, unlike all the preceding minute organs, is limited to a very small segment of the canal. It consists of a number of highly ramified tubes, which are usually termed the *glands of Brunn*, but might preferably be named the *racemose* or *duodenal glands.* These glands occupy that upper part of the small intestine already distinguished as the duodenum ; of which segment they are thus, as it were, the natural index, or the characteristic structure.

The racemose glands are small "conglobate" masses ; which in their size, structure, and position, closely resemble those accessory salivary organs that stud various parts of the mucous membrane lining the cavity of the mouth. Like these "labial" and "buccal" glands, they occupy the sub-mucous areolar tissue : and are therefore best examined by pinning out a piece of the duodenum on some flat surface, with its mucous side downwards, and then carefully removing the serous and muscula. coats. Such a dissection easily exposes them, as small roundish white granules of about the size of a millet seed.

They vary considerably in size and arrangement. Immediately beyond the pylorus, they are of one-tenth to one-eighth of an inch in diameter ; and are present in such numbers, as to form what is almost a glandular layer around this part of the intestine. But lower down in the duodenum, their size dwindles to one-half or one-third of the above : and their scattered grains gradually become more sparing in number ; until, shortly before the termination of its inferior transverse portion, they cease altogether.

On tracing out the structure of an isolated duodenal gland under the microscope, it is seen to consist of numerous lobules; which are aggregated into a single mass (*c c*, *fig.* 272.), by an enveloping layer of fibrous tissue. And on applying a still higher magnifying power, each of these lobules may be again resolved into smaller ones, which resemble a bunch of grapes, and constitute the true or ultimate *acini* of the gland. As seen *in sitû*, these vesicles have a globular or slightly polyhedral form; and a diameter which is about $\frac{1}{500}$th to $\frac{1}{200}$th (on an average, $\frac{1}{300}$th) of an inch. But when separated from each other, they often exhibit more irregular shapes (*d*, *fig.* 273.). They are the terminal dilatations of tubes, which are themselves about two-thirds of this size. On tracing these minute tubes towards the general mucous surface, they will be found uniting with other similar ones, to form larger ducts. The successive union of these with other ducts formed in the same way, and of these larger ducts with their neighbours, gradually causes all their cavities to converge into a single canal of outlet, which is the proper efferent duct of the gland. This duct now passes between the intestinal tubes before described, to open on the free surface of the intestine, in the depressions which intervene between the rudimentary villi present here. The valvulæ conniventes are not permeated by any such ducts. But in all other parts of its surface, the general mucous membrane is pretty evenly studded by their apertures, two or more sometimes passing through it in company with each other.

Fig. 272.



Racemose or duodenal gland, as seen in a vertical section of the duodenum. Magnified 40 *diameters.*

a, intestinal tubes ; *b*, muscular stratum of the mucous membrane ; *c*, *c*, *acini* of the duodenal gland, which occupies the submucous areolar tissue ; *d*, transverse layer of the muscular coat ; *e*, longitudinal layer of the muscular coat ; *f*, peritoneal tunic of the bowel.

Fig. 273.

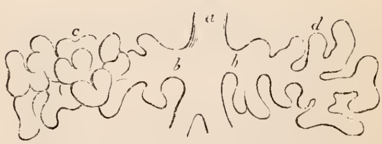


Diagram of the arangement of the lobules of a duodenal gland.

a, duct of the lobule ; *b*, collateral branch of this duct ; *c*, the acini around such a duct *in situ ; d*, the same separated, and the duct unfolded.

Hence each of these glands may be briefly described as a tube, which branches repeatedly, and ends in very minute canals, with somewhat vesicular extremities.

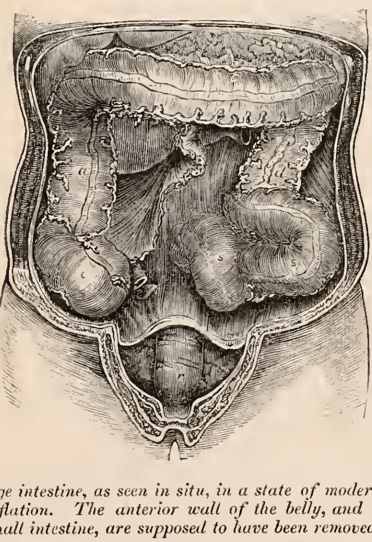
The whole of this involution of mucous membrane is composed of the usual elements ; namely, limitary membrane and epithelium. The former constituent offers no peculiarity worthy of note. The latter consists of a single tesselated layer of cells. These have a polygonal and slightly flattened shape, which somewhat resembles that of the cells lining the smaller branches of the straight urinary tubules. Where the smaller tubes converge to form the efferent duct that perforates the mucous membrane, these cells are exchanged for short cylinders, the structure of which rapidly merges into that of the ordinary columnar epithelium of the general intestinal surface.

As regards the *secretion* of these racemose glands, we can only state that their ducts contain a structureless mucus, which has an alkaline reaction.

With such an imperfect knowledge of its nature, we can scarcely wonder that the office of this fluid remains unknown to us. Like many other animal matters, it converts starch into sugar. But until the precise rapidity and energy of this change have been established, it is impossible to determine how far this action is really comparable to that of the saliva. From the close resemblance between the sub-mucous glands of the mouth and these of the duodenum, many have assumed them to prepare a salivary fluid. But, besides that we are not warranted in regarding the secretion of the buccal glands as identical with the saliva (of which it forms but a very small ingredient), a very moderate knowledge of histology might suffice to indicate the danger of inferring the nature of any secretion from the mere arrangement of the structures by which it is furnished. Hence it must remain for the present undecided, whether this mucus is a salivary or pancreatic fluid; or merely a more concentrated form of intestinal juice, secreted by glands which here reach a higher degree of development than that attained by the short cylindrical tubes of the rest of the bowel.

Large intestine. — The remaining portion of the alimentary canal forms the *large intestine*

Fig. 274.



Large intestine, as seen in situ, in a state of moderate inflation. The anterior wall of the belly, and the small intestine, are supposed to have been removed.

c, cæcum; *a*, ascending portion of the colon; *t*, transverse portion; *d*, descending portion; *s*, sigmoid flexure; *r*, rectum.

(*c a t d s r*, *fig.* 276.) (*intestinum crassum*, Lat.; *gros intestin*, Fr.; *dickes Gedarm*, Germ.): — a name which alludes to the size that is one of its chief characteristics. Beginning at the termination of the ileum, in the right iliac fossa, it passes upwards to the under surface of the liver. Here it turns at a right angle, and runs horizontally below the stomach, to the left extremity of this organ. By a second bend, it here resumes the vertical direction, and then passes downwards towards the left iliac fossa. In this region it undergoes a remarkable curvature, which has the shape of the italic letter *S*. From the lower end of this "*sigmoid*" flexure, it passes obliquely towards the median line; where it terminates in a straight, short tube, that runs vertically through the pelvis to the outlet of the anus. Hence the entire segment of large intestine has the shape of a horse-shoe; and forms a large bend, which is concave downwards, and passes almost round the confines of the abdomen before ending at the inferior extremity of this cavity. While its general arrangement is such, that the intestinal canal, which diverges from the median line at the lower end of the œsophagus, returns to it shortly before terminating in the posterior or lower segment of the trunk.

An accurate measurement of the length and width of this tube is opposed by the difficulties already alluded to in the case of the small intestine. My own observations would indicate an average length of from four to six feet, and a mean diameter of about $1\frac{2}{3}$ to $2\frac{2}{3}$ inches: — the two measurements usually varying inversely to each other, except in the cases of extreme distention or contraction, when both respectively increase or decrease simultaneously. Hence the large intestine has about a quarter the length, and twice the width, of the small. From such an estimate we may conclude that, while its capacity is almost equal to that of the narrower tube, its active surface is scarcely half as large. And even this great difference is much increased by the absence of villi and valvulæ conniventes from the interior of the large intestine.

Like the rest of the canal, the wall of the large intestine is composed of the serous, muscular, and mucous coats; and of vessels, nerves, and lymphatics, which are distributed to them.

The nature and arrangement of these tunics vary, however, in the several parts of the tube. And these differences, aided by others which affect its size, shape, and situation, subdivide the large intestine into the following segments: — the *cæcum*; the *vermiform appendix*; the *colon*, in which we distinguish an *ascending*, *transverse*, and *descending* portion, and a *sigmoid flexure*; and, finally, the *rectum*. The anatomy of each of these will demand a brief notice.

The *cæcum* (*c*, *figs.* 276, 277.) (formerly *blind gut*, Eng.; *blind Darm*, Germ.) is the first and largest of these segments. Its arrangement may be described as due to the fact, that the small intestine, instead of being simply continuous with the large (like the stomach with the duodenum), opens into it at right angles to its axis, and at some distance from its commencement; so as to leave a blind extremity of the larger tube at the site of their mutual junction. The *size* of this *cul-de-sac* generally exceeds that of the remainder of the bowel; it being larger than any other part of the alimentary canal, with the single exception of the stomach. When moderately distended, its diameter ranges from $2\frac{1}{2}$ to $3\frac{1}{2}$ inches; and its length is about as much. Its vertical extent is, however, somewhat arbitrary; since, though defined in part of its circumference by the aperture of the ileum and by the ilio-cæcal valve, it is elsewhere only limited by an imaginary line drawn around the tube at the level of the latter orifice.

The *situation* of the cæcum, in the left iliac fossa, allows it to vary considerably in size, without undergoing any marked change of its relations. Bound down as it is to the fascia over the iliacus muscle by peritoneum and loose areolar tissue, its enlargement merely causes it to displace such portions of the small intestine as may hitherto have shared the occupation of the iliac fossa. After its distention has removed these from its anterior surface, it reaches the anterior wall of the belly in the iliac region; where its size, shape, and contents can be more or less recognized during life, by the ordinary means of physical investigation.

The above dimensions render it obvious that the *shape* of the cæcum is somewhat globular. This shape is, however, modified by the arrangement of its muscular layers; which here begin to offer a peculiarity that is maintained throughout the whole of the colon. The uniform external or longitudinal layer present in the small intestine is here contrasted by one which is separated into three flattened bands, that occupy the side of the tube at nearly equal distances from each other. In the cæcum one of these (and the larger of the three) is anterior; one posterior; and one external. And all three of them become continuous above with the corresponding bands around the ascending colon. Between these slips of muscle, the bowel presents a more or less dilated and projecting external surface; which is again subdivided by transverse constrictions into subordinate pouches or sacculi. On laying open the bowel, and removing the mucous membrane from its inner surface, it may be seen that these transverse constrictions are in reality formed by the circular muscular coat; which gives off projections or incomplete septa, that complicate the general cavity of the tube, by adding a number of supplementary cells. These cells are arranged in three vertical rows; which are separated by ridges, that correspond to the external depressions formed by the longitudinal bands above mentioned. Between these bands, the "*haustra*," or pouches of the bowel possess a muscular tunic of very inconsiderable thickness: the transverse or circular layer being reduced to a thin membranous lamina; and the longitudinal being, as before stated, altogether absent. The close relation of these longitudinal and transverse septa to the length and width of the bowel is well shown by the effect of cutting across or removing its three bands, and then distending the tube by artificial inflation. This obliterates the "falciform folds" or transverse septa; and thus converts the sacculated intestine into a canal, the length and diameter of which are nearly double of what it formerly possessed when retained in its proper shape by its longitudinal bands or "tæniæ."

The *serous* covering of the cœcum is chiefly remarkable from the closeness with which it generally attaches the bowel to the fascia over the iliacus muscle. When the tube is but moderately distended, it covers only its anterior surface. Extreme contraction can, however, render it a more complete covering; and may even produce it into a kind of meso-cæcum behind the bowel. While conversely, great distention of the tube reduces the peritoneum to a partial investment; which occupies but a third, or even less, of the intestinal surface.

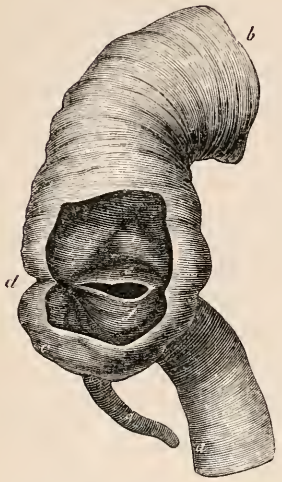
The *mucous membrane* of the cœcum differs in no essential respect from that of the remainder of the large intestine, the structure of which is continued up to the very edge of the valve which severs it from the ileum.

The cæcum has three *apertures*: — one, a large opening by which its cavity is directly continuous with the colon; a second, which communicates with the small intestine, and is guarded by a double valve; and a third, which opens into the slender vermiform appendix.

Ileo-cæcal valve. — The opening into the ileum is situated at the upper border of the cœcum; on its left side, and a little posteriorly. The structures which bound and define this opening are collectively termed the *ileo-cæcal* or the *ileo-colic valve*: — although these names ought in strictness to be limited to those separate portions of the entire intestinal valve which their etymology would indicate.

The arrangement of the intestinal tunics in this valve is best seen by inflating and drying that part of the intestine, which includes, together with the last inch or two of ileum, the cæcum, and the commencement of the colon. On cutting out a piece of such a dried preparation, so as to gain a view of its interior, we see the valve as represented in the accompanying figure (*fig.* 275.) The small intestine, generally inclining slightly upwards as well as backwards, passes towards the cæcum, at what is thus a rather acute angle. Instead, however, of opening into the bottom of one of the sacculi of the cæcum, it selects for its entry the exact site of the deepest and most projecting of those transverse constrictions which project into the cavity of the large intestine. This constriction occupies the inner side of the bowel; and is, as it were, split up by the entering ileum into two laminæ; — an upper and a lower, an ileo-colic and an ileo-cæcal (*e*, *f*, *fig.* 275.) While, at the same time, the hitherto cylindrical calibre of the small intestine is gradually reduced to a horizontal slit or fissure, as it enters this fold.

Fig. 275.



Cæcum inflated, dried, and opened, to exhibit the arrangement of its valve.

a, termination of the ileum; *b*, ascending colon; *c*, cæcum; *d*, transverse constriction projecting into the cæcum from its inner surface; *e f*, valve separating the small from the large intestine; *e*, its horizontal ileo-colic lamina; *f*, its more oblique ileo-cæcal lamina; *g*, the vermiform appendix of the cæcum.

Such a description at once explains the form of the valve: — how each of its segments, for example, constitutes a crescentic membrane, the plane of which meets that of its fellow at an acute angle, and the free edge of which is directed outwards; — and how both end anteriorly and posteriorly in a commissure or fold, that gradually decreases in depth as it passes either forwards or backwards round the intestine.

As regards the details of its construction, each segment of the valve is chiefly formed by the prolongation of a corresponding portion of the circular muscular fibres of the ileum, together with a few proper to the large intestine. The assistance afforded to these by the attachment of the peritoneum and the longitudinal fibres of the ileum, to the fixed margin of each segment, is well shown by the effect of dividing the latter structures. For after such an injury, moderate traction draws out the valve into a surface, which is directly continuous with the lower end of the small intestine; and at the same time converts its horizontal slit into a large elliptical aperture. The difference between the ileo-cæcal and ileo-colic portions consists chiefly in the fact, that the plane of the former is more oblique, and its margin more concave, than that of the latter.

The *mechanism* of this valve may be easily deduced from its structure. In all states short of actual distention, the passive contraction of its muscular walls no doubt insures their contact, and shuts off the cavity of the ileum from that of the cæcum. While any approach towards a more active dilatation of the large intestine — whether of the cæcum, or colon — at once brings about a close apposition of the two portions of the valve. And whatever aid may be given to this mutual apposition of the surfaces of the valve by its own active muscular contraction during life, nothing is more certain than that its closure is essentially independent of any such vital process. For the gradual and equable distention of the cæcum with liquid in the dead subject can also produce this result.

Nor is it difficult to understand how such a closure is effected. The passage of the contents of the large intestine, over either plane of the valve, presses it against the opposite one, so as at once to close its orifice. Besides this, the free margins of the valve form segments of a larger circle than its attached ones. Hence they are disproportionately tightened by the same distending force. In this way, the double curve of each lamina is soon reduced to a straight line, that brings it into exact apposition with its antagonist. So that, within all ordinary limits, the greater the dilating force, the more closely are the two lips of the valve applied to each other.

The only valid exceptions to this rule may be found in those cases in which the ileum and cæcum are filled simultaneously. Such a process of distention necessarily occurs in all cases of mechanical obstruction of the digestive canal below this valve; as a result of the downward flow of the contents of the small intestines. And since it obviously distends the aperture by the application of a counter-force from the side of the ileum, its mechanical action is so simple as to require no further explanation. Its effect may indeed be seen in the cæcum, as usually inflated and dried.*

The function of this valve therefore offers a complete contrast to that by which the stomach opens into the small intestine. For while it affords little or no obstacle to an onward transit of the contents of the canal, it resolutely bars the way to all regurgitation: — an action which we have already seen is exactly reversed by the pylorus. And even in the absence of information respecting the details of its active contraction, its structure entitles us to conjecture, that the greater part of its efficiency depends upon a passive, and therefore permanent mechanism; and not, as is the case with the pylorus, on an intermittent (and vital) shortening of its muscular fibres.

The use of the cæcum is evidently that of forming a receptacle, in which the contents of the small intestine may sojourn for a certain time, before passing onwards into the colon.

* Hence it is scarcely a superfluous caution to add, that in examining such a preparation we ought always to recollect, that the patulous orifice thus seen is in reality an abnormal one, which does not illustrate the mechanism of the valve in the healthy living body.

For not only are its shape, size, and direction such as admirably adapt it to this purpose, but its development in different species and individuals closely corresponds to the degree in which such a delay is advantageous to digestion. Thus the large cæcum of the Herbivora is contrasted, in the Carnivora, by one of but inconsiderable size and development. While there are grounds for conjecturing, that the habitual use of a vegetable diet is capable of increasing its size in the human subject. In all of these respects, however, its development does but parallel that of the remainder of the large intestine. We may therefore defer considering the nature of its secretion, and the changes undergone by its contents, until these segments of the bowel have also been noticed.

The *vermiform appendix* (*g*, *fig.* 275.) which is so named from its resemblance in shape and size to a worm, is a small, smooth, cylindrical tube; that opens into the cæcum below (and rather posterior to) the aperture of the small intestine. Its length varies from one to four or five inches: its diameter from about a fourth to a third of an inch. Its attached end of course shares the situation of the contiguous part of the cæcum. Its distal extremity is usually free; and may hence be found in almost any situation which its length, and that of the short mesentery that binds it down, together allow it to take. Its opening into the cæcum is often partially occluded by a kind of transverse fold or valve.

As regards its structure, the vermiform appendix exhibits all three of the ordinary coats. Its peritoneum is derived from that of the cæcum, and often forms a short fold or mesentery which is prolonged up a part of its length. Its muscular stratum is of uniform and considerable thickness, and is continuous with the three longitudinal bands which give the cæcum its sacculated shape. Its mucous membrane is occupied by tubes and follicles, like those of the colon. And the latter structures are often present in such extraordinary numbers, as to constitute almost a continuous layer of these minute closed sacs. The calibre of the tube, which is in general disproportionately small, is occupied by a sparing quantity of glairy mucus; and occasionally, by small fragments of the ordinary intestinal contents.

The use of the vermiform appendix is unknown. It has been suggested to be a mere relic of the umbilical duct of the fœtus: — an erroneous view, to which allusion will hereafter be made in speaking of the development of the intestinal canal. It is almost peculiar to Man; in whom its situation often causes it to receive small solids in their transit through the cæcum, with the result of their becoming impacted in its narrow cavity. This accident is sometimes followed by inflammation and perforation of the tube, causing fatal peritonitis.

The *colon** (formerly *Great gut*, Eng.; *Grimmdarm*, Germ.), which forms by far the greater part of the large intestine, extends from the ilio-cæcal valve to the rectum. Starting from the right iliac fossa, it passes vertically (*a*, *fig.* 274.) up the posterior wall of the belly, and on the right side of the spine, until it reaches the under surface of the liver. A sudden turn at a right angle marks the end of this *ascending* portion, and the beginning of its *transverse* part. The latter segment, though tolerably horizontal, forms an arch (*t*, *fig.* 274.) with the convexity forwards, so as to pass around the projecting spine and aorta. Below the spleen it merges, by another rectangular bend, into the *descending* colon (*d*, *fig.* 274.) This takes much the same course on the left side of the abdomen as the ascending colon does on the right; and opposite to the crest of the ileum, it ends by becoming continuous with the sigmoid flexure (*s*, *fig.* 274.). The latter portion is attached by a short mesentery to the left iliac fossa; and it terminates in the rectum, at a point corresponding to the left sacro-iliac symphysis.

The relations of each of these segments to the adjacent textures and organs may be easily deduced from their course as described above.

Thus the *ascending* colon lies on the right kidney and quadratus lumborum muscle, from which it is only separated by loose areolar tissue. On its left side, is the psoas muscle; and above it, the vertical portion of the duodenum. In front, it is covered by coils of intestine; or, if sufficiently distended to thrust these away, by the anterior wall of the belly.

The *transverse* colon is almost always in contact with the omentum and abdominal parietes, which it touches in the horizontal line that marks the mutual limit of the umbilical and epigastric regions. Above it, is the first portion of the duodenum; with the stomach, liver, gall bladder, and spleen. Below it, are the coils of the small intestine. Behind it, lie the second and third portions of the duodenum,— the latter covering the aorta. To its posterior surface is attached the *transverse meso-colon;* which connects this part of the intestine with the wall of the belly, by a double fold of peritoneum, that splits to enclose the tube. The double lamina formed by the reunion of these two layers of serous membrane in front of the bowel, is continuous, at the lower border of the great omentum, with the similar process that descends from the great curvature of the stomach.*

The *descending colon*, like the ascending, lies on the left kidney and the left quadratus lumborum muscle, and is covered by a variable quantity of the small intestine.

The *sigmoid flexure* is much more frequently in contact with the abdominal wall than the preceding portion of the colon. And its freedom of movement, to which this contact is partly due, also allows the bowel to deviate considerably from its ordinary curvature and

* This Greek word, which has been adopted into most of the modern languages, is derived indifferently from κῶλον, *membrum*, and κόλον, *alvus* (παρὰ τὴν κοιλότητα).

* See Art. Peritoneum.

position. The shape of this bend corresponds so exactly to its name, that it is scarcely necessary to bestow any further description upon it. Its curve is chiefly in the vertical plane; though a slight lateral curvature is almost always present, and is easily exaggerated into a much more distinct bend by the mobility of this segment of the canal.

The use of the sigmoid flexure seems to be that of forming a receptacle for the fæces:— a receptacle of which the shape and arrangement are such as to spare the rectum and its sphincter from much of the pressure and weight against which they would otherwise constantly have to contend. When full, the convexity of its lower bend often projects below the iliac fossa, so as to descend into the pelvis. Indeed, the whole of the colon is very liable to displacement from the various positions just assigned to it:—prolonged distention by its accumulated contents, or the mechanical force exerted by the pressure of stays externally, or of tumours internally—being all capable of altering its relations, and even confusing its different parts* with each other.

The colon retains the sacculated shape assumed by the cæcum. Its size undergoes a progressive though slight decrease, from its commencement in the cæcum to its termination in the rectum. Its peritoneal coverings reach their minimum in the ascending and descending portions; where they only cover about two-thirds of the moderately distended bowel, and leave its posterior or attached third quite unoccupied by this membrane, and connected by loose areolar tissue to the subjacent parts. Hence it is these portions of the bowel which are selected in the operation for artificial anus.† But, just as great distention can always increase this uncovered portion, so, *vice versâ*, excessive contraction may reduce it to a mere line, or may even develope a kind of short meso-colon in connection with either of these parts. The muscular strata which cause its sacculated shape, also retain the arrangement existing in the cœcum. But on the transverse colon, the internal longitudinal band becomes inferior. And on the sigmoid flexure, this and the posterior band generally merge into a single one. The latter change is accompanied by an indistinctness of the transverse sacculi themselves.

Throughout the whole of the large intestine, the peritoneum is here and there developed into peculiar, processes, called the *appendices epiploicæ* (ἐπίπλοον, *omentum*). These are short pouches of the serous membrane, which generally form flattened duplicatures or folds. They are prolonged from the peritoneum covering the surface of the intestine itself; and are therefore absent from that portion of the rectum, or terminal segment of the large intestine, which does not receive any covering of this membrane. Their number, size, and arrangement, are liable to great variety. Sometimes they are so numerous, as to form a single or double row along the free surface of the bowel. In other instances they are very few and imperfect. Their size is so far related to the state of the bowel, that, like most other processes of peritoneum, they are enlarged by its contraction, and diminished by its distention. From their contents, which consist of areolar and adipose tissue, they would seem to be small reservoirs of fatty matter. Hence in cases of remarkable obesity, their size is much increased. Indeed they sometimes acquire a length of one or two inches; and have even been known to encircle and strangulate the bowel.

Movement of the large intestine.—The exact nature of the movement which is executed by the muscular coat of the large intestine can at most only be conjectured from some of its attendant circumstances. Like that of the preceding segment of the canal, though its general mechanism is obvious, its details remain unknown.

As regards the investigation of the contents of this intestine in its ordinary situation during life, all that can be stated is, that, even in health, they include a quantity of gaseous matter; which usually maps out the cœcum, and more or less of the colon, with tolerable distinctness, from the less resonant convolutions of the small intestine.

After death, the quality and quantity of these contents are so much affected by the nature of the previous food, the mode of dying, and a variety of kindred causes, that scarcely any general proposition can be laid down with respect to them. But on the whole, we usually find, that in addition to much gaseous fluid, the cæcum of the healthy subject is partially distended by pultaceous or semi-fluid contents. While the colon is occupied at various points of its length by matter, the fæcal character of which is still more distinct, and the consistence of which gradually increases as it approaches the rectum.

Where these rudimentary fæces are very imperfect, scanty, and interrupted, they only occupy some of the sacculi or cells of the bowel, leaving its central or general calibre in an empty state. But when better developed, they form what is termed a "figured" mass. This consists of a kind of central rod, that corresponds to the general axis of the tube; and of processes that come off from the sides of this axial portion, and are contained in the rows of pouches formed by the wall of the bowel. In short, the solid and continuous fæcal substance forms a tolerably perfect cast of the bowel;—a cast in which the sacculi of the colon are "figured" as projections, themselves isolated by depressions corresponding to the intersections of its longitudinal and transverse bands.

The characteristic shape thus possessed by the solid contents of the colon, is often retained by the fæces which have been forced through the rectum in the natural process of defæcation. And although it is often absent,—the con-

* See *Abnormal Anatomy.*

† Other things being equal, the left or descending portion is preferred: on account of a larger extent of the canal being thus left to be traversed by the intestinal contents.

sistence of the fæces being such* as to mould them to the cylindrical form of the last-named portion of tube through which they have to pass—still it occurs so frequently in Man, and so universally in many of those Herbivora in whom we can best study the phenomena of a highly developed large intestine, as to afford a valuable testimony to the natural action of this part. It is therefore difficult to avoid believing, that the individual sacculi of the colon, or at least of its later segments, retain the fæces for a considerable period of time; during which they so far complete the action of the large intestine upon these its contents, as to leave nothing for its remaining segments to effect, save their mechanical propulsion towards the outlet of the canal. To this intermittent action of the muscular coat in respect of time, we may probably add a similar interruption as regards space. In other words, the interrupted and irregular manner in which the sacculi are often occupied by solid fæces, entitles us to suspect, that different lengths of the intestine can act independently of each other. But it is difficult to hazard a conjecture as to whether the contraction of the falciform transverse folds ever really shuts off portions of the tube into distinct cavities. The central axis of the figured evacuation is, however, often so slender, or even interrupted, as remarkably to corroborate such a view. And some authors have assumed that the cæcum, during its digestive act, is isolated from the ascending colon by a vigorous contraction of that large fold which is prolonged from the frœna (or anterior and posterior extremities) of the ilio-cæcal valve.†

The little information afforded us by direct observation on the movements of the intestine, confirms what is thus vaguely suggested by the appearances of its expelled contents. The highly developed large intestine of the living or newly-killed rabbit, rarely exhibits any noticeable movement whatever, when first exposed to the air. By and bye, however, a kind of irregular peristalsis comes on. But this is nowhere quite so energetic as that seen under similar circumstances in the small intestine; and is generally very feeble in the cæcum.* And in this movement, as in that produced by mere local irritation, we may notice the peculiar character before attributed to the contraction of unstriped muscle generally;—viz., that of diffusing itself over a time and space greater than those occupied by the irritation which has excited it. As regards the details of this vermicular action, certain sacculi contract and dilate alternately; the transverse constrictions between them sharing in the same movement. This alternate movement is often accompanied by an irregular contraction of the longitudinal bands; which is sometimes carried to such an extent, as to shorten the tube, by approximating and dilating certain of its cells. And even where the effect of the local irritation survives its cause, so as to excite a continuous movement which proceeds along a considerable length of intestine, still it rarely affects all the cells of the bowel exactly alike; but often passes lightly over one or two, to bear with increased intensity on those which immediately succeed them. Very similar movements are produced by galvanizing the solar plexus which gives off the nerves to the large intestine.

On the whole, therefore, the greater solidity of the contents of the large intestine implies a greater resistance to the contraction of its muscular coat. And the structure of this coat shows no proportionate increase, but rather a decrease of strength. Hence we might almost conjecture, that the general movement of the small intestine is here exchanged for one which is slower, feebler, and hence less effective: and which, besides being much weaker, is possibly interrupted by longer periods of rest.†

But it is probable that this comparatively feeble character of the general movement of the large intestine is capable of being more than compensated by that heightened efficacy which the peculiar arrangement of its muscular coat can concede. The thin muscular stratum that forms the wall of its numerous pouches, is evidently capable of assuming a much smaller surface, in obedience to the thick and powerful bands of its transverse and longitudinal coats. Indeed, the simultaneous contraction of these two sets of fibres would convert them into what would form, for the time, a very thick and powerful expanse of unstriped muscle, capable of obliterating the entire calibre of the intestine.

In this way the same muscular apparatus

* The consistence of even a figured evacuation is sometimes so slight, as to render it highly probable, that a general relaxation of that segment of intestine which originally contained the fæcal mass has accompanied the propulsive contraction of the part immediately behind it. Such an apparently co-ordinate relaxation of the muscular coat may be frequently noticed in that vermicular movement of the small intestine which is seen shortly after death. An occurrence of this kind seems almost the only way in which one can account for the fact, that soft and semifluid fæces frequently retain the form of the colon, after passing through its falciform folds. Whether such an action is ever effected by a contraction of the longitudinal bands simultaneously with a relaxation of the circular or falciform folds, it is impossible to determine. But from their mechanism, and from the above appearances of the fæces, it would seem more probable that both these classes of fibres relax simultaneously.

† Energetic contraction of the transverse fibres of this valve would obviously aid in its occlusion; though we have already shown it to be probably independent of all active muscular force.

* The contractions by which this part responds to a local stimulus are far more feeble, slow, and uncertain, than those obtained in any other part of the canal,—the stomach not excepted. This character seems to be a direct result of the tenuity of the muscular coat, which also attains its maximum here. An incident which I have remarked in one or two cases of intestinal obstruction appears to be partly explained by the same structural peculiarity. In these instances, though the stricture was seated in the descending colon, the dilatation and rupture that formed the immediate cause of death occupied the cæcum.

† Compare pp. 343, 344.

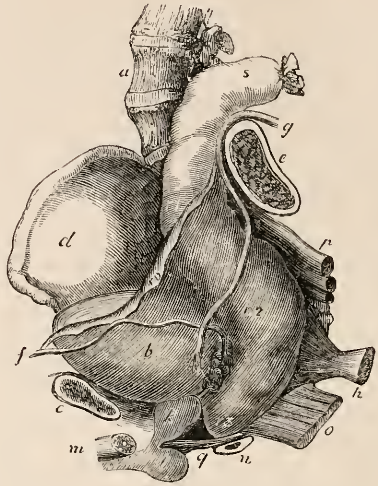
which generally concedes to the contents of the large intestine a long delay, and a slight movement over a large absorptive surface, would still be quite capable of effecting their rapid and vigorous expulsion, when required to do so. Nay, more, since much of this expulsive act seems, as it were, removed from the sacculi themselves, and concentrated in the bands around them, we may conjecture that the mechanism of these latter contractile masses is also specially concerned in the nervous part of the process. At least, it is not impossible, that the irritation or stretching of these two sets of muscles (which can be effected only by the general distention of the calibre of the tube, and not by the local distention of its cells) may constitute the immediate stimulus of the evacuation of the whole large intestine, or of any particular segment.

The *mucous membrane* of the colon may be described as only differing from that of the small intestine in the fact that it is somewhat thicker, and quite devoid of villi. Its more numerous *tubes* are about one-third longer than those of the small intestine; and their diameter seems to be, in general, still more increased. Its *solitary follicles* are also more numerous, and of larger size. And the depressions which mark the site of each on the internal surface of the bowel are here represented by a distinct pit; which leads by vertical, or even somewhat divergent sides, to the follicle that occupies its base. But the secretions of these structures, and the cell-growth which lines them, do not present any noticeable difference from their analogues in the small intestine.

The *rectum* (*r*, *fig*. 274.; *r* 1, *r* 2, *r* 3, *fig*. 276.) (formerly *straight gut*, Eng.; *Mastdarm*, Germ.), which intervenes between the sigmoid flexure of the colon (*s*) and the anus (*n*), forms the terminal segment of the large intestine. It has received the above name from the comparatively direct course which it takes. Its length is about seven to eight inches. Its width is at first only equal to that of the small extremity of the colon, with which it is continuous: but gradually increases, so as to form a kind of dilatation or pouch in the immediate neighbourhood of its lower aperture. Here it suddenly contracts to the narrow orifice of the *anus;* which is situated in the perineal space, that closes the pelvis, and forms the lower extremity of the trunk.

Strictly speaking, however, the rectum is by no means straight. Beginning at the left sacro-iliac symphysis (*e*, *fig*. 276.), it first passes obliquely downwards and to the right side, towards the median line of the trunk; which it reaches at a point that nearly corresponds to the body of the third sacral vertebra (at *r* 1, *fig*. 276.). And though, from hence to its termination, it continues to occupy the middle line, still as it rests upon the concave anterior surface of the remainder of the spinal column, it assumes a curve similar to that of the sacrum. It thus acquires a second and more remarkable bend (at *r* 2, *fig*. 276.), which is convex backwards. Finally, at the tip of the coccyx, it quits the antero-posterior direction given it by this bone; and, bending suddenly

Fig. 276.



The viscera of the adult male pelvis, as seen after the removal of the right innominate bone: showing the situation and relations of the rectum.

a, fourth lumbar vertebra; *b*, bladder; *c*, symphysis of the pubis; *d*, inner surface of the left os ilii; *e*, sacro-iliac articulation; *f*, vas deferens; *g*, ureter; *h*, spine of the ischium sawn through, and left attached by the coccygeus muscle; *i*, left vesicula seminalis; *k*, prostate gland; *l*, bulb of the urethra; *m*, left corpus cavernosum divided at its root; *n*, anus; *o*, levator ani cut across near its attachment to the coccyx; *p*, sciatic nerves and vessels; *q*, fibres of levator ani passing round the lower end of the rectum; *r*, rectum, 1, 2, 3, its first, second, and third portions; *s*, sigmoid flexure of the colon; *r v*, peritoneum forming the left side of the recto-vesical pouch.

downwards at a right angle, becomes vertical for a very short distance (at *r* 3, *fig*. 276.) prior to ending in the anus.

The above successive changes in its direction are associated with others, which affect its relations to the peritoneum and to the surrounding structures. In accordance with these, it is usual to describe the rectum as subdivided into three portions.

The *first or oblique segment* (between *s* and *r* 1, *fig*. 276.) is about 3½ inches long. It is covered on every side by peritoneum; which, at its commencement, attaches it to the pelvis by a short meso-rectum, very similar to the meso-colon of the sigmoid flexure.* It lies on the sacrum, the upper border of the pyriformis muscle, and the sacral plexus. In front of it is the bladder, from which it is generally separated by some convolutions of the small intestine. On either side

* This meso-rectum is sometimes so long, as to give this segment of the bowel a mobility (and often a shape) very similar to that of the neighbouring sigmoid flexure itself.

it is related to the ureter, and to the branches of the internal iliac vessels.

The *middle or arcuate segment* (*r* 2, *fig.* 276.) scarcely exceeds 2½ inches in length. It lies on the sacrum and coccyx; to which it is attached by a loose areolar tissue, that usually encloses much fat. The peritoneum, which invests a small part of its lateral surfaces above, soon becomes limited to its anterior surface as it descends; and ceases altogether at a distance of about an inch from the termination of this part of the bowel. This incomplete serous covering is, in fact, the lower extremity of a process of peritoneum, which is called *the recto-vesical pouch* (*r v*, *fig.* 276.). The apex of this, below, corresponds to the point where the membrane is reflected from the anterior surface of the rectum, to the neighbouring posterior surface of the bladder. Hence the front of the bowel, which, above, comes into contact with the distended bladder, or with any convolution of small intestine that may chance to occupy the recto-vesical pouch, touches, below, the anterior part of the base of the bladder. This it does in a triangular space, that is bounded on each side by the vesicula seminalis (*i*, *fig.* 276.), and behind by the pouch aforesaid:—a space which therefore corresponds to the "*trigone vesicale*" on the inner surface of the bladder; and marks a region, where this viscus may be punctured through the rectum, without any injury to the serous membrane. On each side of this part of the rectum, is a lamina of pelvic fascia which supports it; and externally to this is the coccygeus muscle, which descends from the spine of the ischium (*h*, *fig.* 276.) to the border of the coccyx.

The *third or terminal portion* of the bowel (*r* 3, *fig.* 276.) is about 1½ inches long. It is surrounded, above, by areolar tissue loaded with fat: below, by the sphincter ani externus (at *n*); and by the levator ani (*o* and *q*) which descends from the pelvis to mingle its fibres of insertion with those of the former muscle. In front of it are the prostate (*k*, *fig.* 276.) and the membranous portion of the urethra in the male, the vagina in the female: behind it, the tip of the coccyx in both sexes. The degree in which the prostate projects into the rectum will of course vary, both with the size of this gland, and with the amount of distention to which the tube itself is habitually subjected. Where its distention is very great, the flaccid intestine sometimes appears almost folded around the prostate gland, so as to offer a kind of pouch on either side of it.

As regards the *structure* of the rectum, its peritoneal coat has already received a sufficient description. Its muscular tunic differs remarkably from that of the colon. In place of being divided into three bands, the fibres of the longitudinal coat are again collected into a single uniform expanse, that surrounds the whole of the tube. And both it and the transverse layer are very much increased in thickness. Thus even in the upper part of the rectum, the muscular coat offers a total thickness which at least doubles that of the colon; while near its termination, it is scarcely less than four times as thick. The fibres themselves are of a redder colour, especially the transverse; and near the anus, they are mingled with the striated elements of the adjoining voluntary muscles. And that distant analogy which the rectum seems to offer the œsophagus in all these respects, is rendered somewhat closer by the presence of numerous folds of mucous membrane, which the mere passive contraction of its muscular tunic appears generally to produce. In short, it would hardly be an exaggeration to say that this, the last segment of the digestive canal, resumes not only the median position, but even the structure and action, of the first.

Muscles of the anus.—The muscular apparatus that guards the lower outlet of the rectum, consists chiefly of two sphincter muscles, which close the orifice of the anus by their contraction. Of these, one, the *sphincter ani internus*, which is situated within the bowel, is little more than a thickening of the proper transverse or circular layer of its muscular coat. It lies immediately beneath the mucous membrane, and consists of the ordinary unstriped fibres, which retain their usual pale colour. The other, the proper sphincter, or the *sphincter ani externus*, is a deep-red mass of striated muscular fibre, which surrounds the lower extremity of the rectum (at *n*, *fig* 276.), including the preceding structure. Its form is elliptical and concave; so that its outer border occupies a higher level than its inner one. Hence it receives the end of the bowel as it were into a shallow funnel; and, on contracting, occludes its cavity by the pressure of what is a surface, and not merely an edge, of its plane of fibres. Its outermost bundles arise from a tendinous structure which is prolonged from the tip of the coccyx; and they pass forwards, on both sides of the bowel, to reunite in the central tendinous point of the perinæum. Its innermost or lowest fibres are attached to a dense subcutaneous areolar tissue that lies before and behind the anus. In the female, they interlace anteriorly with those of the constrictor vaginæ, by what is often a distinct decussation.

It is chiefly through the intervention of this sphincter that the *levator ani* muscle is connected with the lower extremity of the rectum. The fibres of this large expanse of striped muscular substance descend from their pelvic origin*, with an inclination backwards, to reach the lower orifice of the cavity of the pelvis, which they assist to close. In front of the rectum, a certain number of them are inserted into the tendinous and areolar tissues which here occupy the middle line of the perineum; and these join more or less directly with the attachment of the external sphincter in the same situation. Behind the rectum, a considerable plane of the more posterior fibres

* For a fuller description of the origin and relations of the above muscle, the reader is referred to the Article Pelvis.

of the levator passes around the tube, returning upon itself in the similar portion from the opposite side, so as to sling and sustain the canal. Between these anterior and posterior slips, is a median portion; which descends to be inseparably united with the upper and outer rings of the external sphincter itself. And besides interlacing with the striped fibres of this muscle, it may generally be traced sending off a certain number of its scattered bundles, to decussate and disappear amongst the unstriped fibres of the longitudinal and transverse layers of the rectum just at their termination.

Movements of the rectum.—The contraction of the muscular coat of the rectum, like that of the other segments of the digestive tube, has for its object the onward propulsion of its contents. But since the rectum ends the intestinal canal, it forms the portal by which these contents are altogether dismissed from the body. Health and comfort alike require that this act of dismissal should be both intermittent and infrequent. While the mere consistence of the fæces is generally such as to demand the application of a comparatively powerful force in order to effect their rapid removal. Hence the entire mechanical action of the rectum is naturally divisible into two stages:—one which propels, and one which expels, the various substances occupying its interior. The latter of these two processes is called *defæcation;* and, as we shall see, involves the aid of various agents which are strictly extraneous to the bowel itself.

Those movements of the rectum which are seen in living or newly-killed animals, can only be regarded as confirming the conclusions that might fairly be inferred from the much greater thickness of the muscular coat in this particular segment of the large intestine.

When empty, the bowel remains in a state of rest, from which it can scarcely be aroused to peristalsis by the application of any local irritation. But when occupied by a moderate quantity of fæces, it will often respond to a direct mechanical stimulus; and still more energetically to the electrical irritation of its nerves. On applying the rapid and powerful shocks of the electro-magnetic machine to those large branches of the sympathetic which are distributed in the muscular coat of the rectum, a violent contraction of this tube frequently occurs. In this intense but irregular movement, we may generally observe a shortening and a constriction:—acts which no doubt represent the specific contractions that form the functions of the longitudinal and transverse fibres respectively. Thus the bowel suddenly becomes straighter and shorter; and hence appears as though it were jerked downwards towards its most fixed point at the lower opening of the pelvis. This shortening is generally accompanied by a less violent and more uniform movement:—in short, by a peristalsis; which offers the ordinary progressive constriction, and is evidently the principal agent in the propulsion of the fæcal pellets. But both of these movements are very irregular. The former commonly alternates with a relaxation, which appears to pull the rectum upwards, and exaggerate its curves. While the latter occupies various parts of the bowel with very unequal intensity and duration; and, occasionally, even seems to take a retrograde course. In most of these details, we may observe the same close analogy between the rectum and the œsophagus, which has already been remarked in their median and terminal situation, and (to a lesser degree) in the nature and thickness of their muscular coat.

The normal movement of the bowel differs from the above in the fact of its being a more exact and co-ordinate action; and, therefore, a much more effective one. But while observation and experiment both agree in representing it as a peristalsis, which is quite capable of slowly expelling fæces of moderate consistence, nothing is more certain than that it is rarely called upon to exert such an independent and unaided force.

Under all ordinary circumstances, its influence is assisted by the action of various voluntary muscles. These may be divided into two classes, which differ in their situation and action.

The first are those large planes of muscle which form the anterior, lateral, and superior, walls of the belly; and thus, by their contraction, exert a forcible pressure on the intestines contained in this cavity.

The second are the similar structures that close the outlet of the pelvis. These have for their office to support the end of the canal. And their muscular nature enables them to effect this support by a texture, the passive or active contraction of which can always increase the reaction or resistance to the abdominal pressure in exact correspondence with the varying demands made upon it. They thus fix the end of the intestinal canal, while it is being emptied of its contents by the pressure of the muscles of the belly.

The mechanism of the abdominal pressure having already been described in treating of the act of vomiting*, but little need here be added with reference to the special conditions under which it is called upon to aid that of defæcation. Of course the chief of these conditions consists in the application of a stimulus to the large intestine itself. And though any irritation of the mucous membrane of the rectum seems capable of producing that violent straining which marks the exertion of the abdominal pressure, still its strictly co-ordinate character is well illustrated by the preference apparently shown to a stimulus which acts directly on the muscular fibres of the bowel themselves. Thus a mechanical distention of the rectum appears to be a more efficient stimulus to the total expulsive act than the application of any ordinary irritant. While, *vice versâ*, there are good reasons for conjecturing, that mere distention of the belly is capable of arousing a sluggish large intestine to expel its contents.† And a

* See p. 316.

† Such a "reflex action," from the animal to the organic muscle, may perhaps explain the operation of one of the ordinary remedies against constipation;

still more frequent association of movement is probably exemplified in the tenesmus produced by dysentery and other disorders, which involve great irritation of the rectum. For the sensations of the patient, and the uncontrollable impulse which follows them, seem to indicate that the irritation of the mucous membrane is often accompanied by violent contraction of the muscular coat of the intestine, both of which unite to excite the subsequent abdominal pressure.

The nature of the contents of the rectum greatly affects the degree in which the muscles of the abdomen are made to assist in their expulsion. When these contents consist only of gases and liquids, they require so little of this aid, as to be sometimes expelled without it. But the extrusion of hard scybalous evacuations often demands the help of abdominal pressure, to an extent such as involves all the viscera of the trunk, and seriously obstructs the flow of blood in the larger veins of the head and thorax.

As regards the levator ani muscle, its origin and insertion, together with the course taken by its fibres, leave no doubt as to what must be the direct effect of its contraction. It raises the end of the rectum, together with the ligamentous structures of the perinæum anteriorly, and the coccyx posteriorly. But as the time of this action seems exactly to coincide with the exertion of the abdominal pressure just alluded to, the degree in which it really raises these structures can only equal the surplus of its force over that of the muscles of the belly. Hence it may be doubted whether the muscle generally does more than fix the bowel: an effect which is, however, of the highest importance to the mechanism of defæcation. The influence of the neighbouring perinæal muscles is still more obscure.

Such being the known agents of the process of defæcation, we may next attempt to sketch the course of its phenomena.

The ordinary peristalsis of the large intestine propels into the rectum a variable quantity of fæces. These, after a longer or shorter sojourn in its first or second portions, excite an active peristaltic contraction of its muscular coat. In general it is only when they reach the lower extremity of the bowel, that the abdominal pressure adds to this peristalsis its far more powerful expulsive force. The combined effect of both these actions urges the fæcal mass against the external sphincter, which relaxes at this instant, by a voluntary effort, so as to permit the extrusion of the descending mass: a small portion of the loose mucous membrane being at the same time generally everted around it.

A variable length of fæcal substance thus passes through the orifice of the anus. The continuity of the descending mass being finally interrupted, the act of respiration* is resumed; the abdominal pressure ceases; and at the same time, the contraction of the levator ani, aided by that of the rectum itself, returns the projecting extremity of the bowel into the pelvis, by a kind of sudden and forcible retraction. The latter act, in which both of the sphincters may be presumed to play an important part, often subdivides a continuous fæcal mass; returning the upper segment thus cut off into the cavity of the rectum which it was just leaving. The total duration of the expulsive act appears to be chiefly determined by the consistence of the fæces, the velocity of their transit, and the exigencies of the suspended process of respiration itself.

The *mucous membrane* of the rectum is connected with its muscular coat much more loosely than that of the colon. Owing to this circumstance, it generally exhibits numerous folds. Most of these are mere temporary results of the passive contraction of the muscular coat. And in correspondence with such an origin, they are very irregular in size, number, and position. They are, however, more frequently found occupying the dilated lower end of the bowel, where they take what is usually a longitudinal direction.

But in addition to such casual and temporary folds, Mr. Houston* has described others, which he states to have a definite direction and situation, as well as a more permanent character. According to this anatomist, three is the number of these folds or valves usually present. The largest and most constant of the three projects from the anterior wall of the rectum, opposite to the base of the bladder, and about three inches above the anus. The valve next above this springs from the left wall of the bowel, about midway between the last and the third or uppermost fold. This latter projects from the right wall of the upper end of the rectum. The shape of all three is nearly semilunar: their depth about half an inch; and they are fixed by a convex border to about half the circumference of the intestine. And Kohlrausch† has described a fold which tolerably answers to the fourth and least constant of those mentioned by Mr. Houston. He states it to be always present, as a transverse projection from the posterior wall of the rectum opposite the middle of the coccyx. In general it contains no muscular fibres: but rarely these may even encircle the bowel, as a continuous ring or third sphincter, which forms the lower boundary of a dilated and sacciform segment of the rectum.

As regards these folds, we may point out, that their usual situation corresponds to the most prominent parts of those three curves of the rectum which we have already alluded to. Thus the third answers to that convex mucous surface which marks the

namely, the application of a wet bandage tightly around the belly.

* The way in which this act is affected during the exercise of abdominal pressure has already been explained at p. 316.

* Dublin Hospital Reports, vol. v. p. 163.

† "Zur Anatomie und Physiologie der Beckenorgane," Leipzig, 1854; also Valentin's "Bericht ueber die Leistungen in der Physiologie" in Canstatt's Jahresbericht, 1854.

transition of the sigmoid flexure of the colon into the rectum; the second indicates the spot where the bowel reaches the median line of the sacrum; and the first is nearly opposite to its bend in the hollow of the latter bone and the coccyx. And frequent as their presence undoubtedly is — and important as they therefore are with respect to the surgery of the rectum, — it may still be doubted whether they possess those characteristic anatomical features that would alone entitle them to rank as true permanent folds, like the transverse or falciform septa which isolate the several pouches of the large intestine. For, unlike these, they are not only somewhat irregular in number and position, but are effaced by complete distention of the tube. And, finally, they appear to contain not a trace of the proper transverse stratum of unstriped fibres. Hence they probably express a mere passive arrangement of the loose mucous membrane; — a relaxation which is perhaps chiefly due to contraction of the powerful longitudinal layer of the muscular coat of the bowel.

In the rectum, the muscular lamina of the mucous membrane resumes its usual thickness. At the lower part of the bowel, the skin and mucous membrane become continuous with each other. But, as might be expected from the great dissimilarity of these structures, there is a distinct line of demarcation between the two. Their junction is situate, not exactly at the anus, but at a point from two to four or five lines above this aperture. Here the skin terminates by a wavy margin, having a distant resemblance with that dentate edge, by which the thick white epithelium of the œsophagus adjoins the delicate pink mucous membrane of the stomach. And the apex of each of these waves usually corresponds to the starting point of a longitudinal fold of mucous membrane; which, after proceeding a short distance up the bowel, either becomes indistinct and disappears, or is crossed and effaced by others that take a different direction. It is nearly in this situation that Kohlrausch * describes a thin layer of unstriped muscular fibres, lying between the sphincter ani internus and the mucous membrane. Traced upwards from their intimate union with the latter structure, these fibres are seen to take a longitudinal course; and to end, about one and a half inches above the aperture of the anus, by joining the layer of circular fibres immediately external to them. Regarding these latter as their origin, it is evident that their action would raise the mucous membrane, and oppose its prolapse. Hence they are described as forming a "*sustentator tunicæ mucosæ.*" Below its junction with the mucous membrane, the moist skin possesses its ordinary structure. And around the anus, it is occupied by numerous hair bulbs; as well as by sebaceous follicles, which pour forth a large quantity of a peculiar odorous secretion.

The *contents* of the large intestine are of two kinds. The first is a mass which, usually of a semifluid consistence, ranges from the state of a thin liquid to that of a hard friable solid. This mass, when evacuated from the rectum, constitutes the fæces, ordure, or excrement. The second is an elastic or gaseous fluid, which occupies the intestine in very variable amount, and unless its quantity be excessive, is not necessarily or regularly expelled at all.

Fæces. It will be some clue to the composition of the fæces if we recollect, that the large intestine so far resembles the small, as to justify our inferring that it continues the various metamorphoses which the contents of the canal begin to undergo in its upper segments. These metamorphoses are due, partly to a spontaneous decomposition of the alimentary substances themselves, partly to changes set up by the various secretions mixed with them. And they are accompanied by processes of absorption and secretion, which may probably be regarded as in some degree peculiar to this segment of the tube. Of these two processes, that of absorption seems chiefly destined to deprive the intestinal contents of their more watery and soluble parts. While the act of secretion pours forth fluids which, from their proximity to the end of the bowel, may be assumed to be, in great extent, excrementitious. The matters thus excreted may be divided, histologically, into two chief constituents: — a structureless alkaline fluid which is furnished by the tubes; and a scaly epithelium, which is a desquamation from the mucous membrane of the rectum.

But it would be wrong to suppose that the whole of the processes which engage the contents of the large intestine can be comprehended in three such acts of metamorphosis, absorption, and secretion as those just alluded to. On the contrary, each of these three exerts its usual complex reaction upon the other two. Thus the soluble results of metamorphosis undergo absorption, as do also some of the substances secreted. The fluids secreted into the bowel no doubt modify the spontaneous changes which engage its contents. And, finally, the slow transit of these contents along the intestine is accompanied by the precipitation of insoluble matters from the various secretions of the upper segments of the canal, prior to their expulsion from its lower orifice.

It has indeed been alleged, that the cœcum is the seat of a special metamorphosis, which repeats, as it were, the process of gastric digestion: — that its mucous membrane pours out an acid secretion, which is capable of dissolving certain constituents of the food preparatory to their absorption. But a closer examination dispels this view, and assigns to this segment an humbler office, which is closely analogous to that of the neighbouring portions of the canal. Its tubes, which have precisely the structure of those found elsewhere, pour out an equally alkaline secretion. Its infusion, whether acidulated or otherwise,

* *Loc. cit.*

has no higher solvent power over albuminous substances than that possessed by the similar fluid prepared from pieces of ileum or colon. While the strongly acid reaction of its contents in many herbivorous animals is sufficiently explained as due to that lactic fermentation, which the various starchy substances are so apt to undergo when exposed to spontaneous decomposition at the temperature (about* 103°) of the intestinal canal. Consistently with such an explanation, this acid reaction is found chiefly or exclusively in those parts of the fæcal mass which are not in contact with the alkaline mucous membrane, and is by no means limited to the contents of the cœcal pouch.

We may therefore regard the fæces as composed chiefly of two constituents: — which are derived, the one from the food taken by the animal, and the other, from the secretions of its digestive organs. And in like manner, we may premise what follows by stating, that the composition of any particular excrement will always depend on the nature of the food, the state of the secretions, and the nature and amount of the metamorphoses which both these constituents have together undergone.

Physical properties of the fæces — Subject to circumstances so numerous and fluctuating, it is obvious that the physical properties of the fæces must vary extremely in different subjects. Their ordinary colour, odour, form, size, and consistence are so well known, as scarcely to require any special description in this essay.

As regards the two first of these characters, the contents of the small intestine are distinctly fæcal. But it is only in the cœcum, where both their colour and odour become much more marked, that the fæces usually begin to acquire a solid consistence. Their form and size is dictated, partly by the shape and diameter of the bowel (as already alluded † to), and partly by the degree in which their consistence has been augmented by the absorption of their watery parts. Where their solidity is much increased from this latter cause, the act of expulsion has little influence in modifying their form. The way in which it usually does this has been previously pointed out.

The odour and colour peculiar to the fæces have been ascribed, by some authors, to the bile which enters into their composition; by others, to the fluids which are poured out into the intestinal canal from the blood-vessels occupying its mucous membrane. It is, however, probable that they are not due to either of these causes exclusively, but depend rather on a combination of both; and are further modified by that admixture of altered (not to say decomposing) food, which forms so large a constituent of the excrement.

Thus, that they depend to some extent on the bile, is well shown by those cases of jaundice, in which a deficient secretion of this fluid, or an obstruction of its normal channel, has arrested its flow into the intestine. For in such instances, the ordinary brownish yellow tint, and fæcal smell, proper to the excrement, are exchanged for a greyish white colour, and an intensely putrefactive odour.

But it is certain that, unless the bile be poured out in excessive amount (as after the exhibition of mercury *), or conveyed through the bowels with unusual rapidity (as in diarrhœa and purging), it is but a small fraction of its total quantity that escapes re-absorption, so as to be found in the fæces. This statement especially applies to the meconium which occupies the intestine of the fœtus. At any rate, this substance contains but little of the acid or the colouring matter of ordinary bile.

Now, the preparation of excrement by the fœtus, and by hybernating or starving animals, is a satisfactory proof that its specific fæcal characters are not essentially due to any modification of the alimentary matters contained in the intestinal canal. And since the bile forms but a small portion of its mass, it is evident that much of it must be derived from the secretions of the digestive tube itself, and that its properties must be partially due to the same source. Indeed, this intestinal constituent, which is probably always a large ingredient of the fæces, becomes, in the hybernant and the fœtus by far the largest: — so much so, that the dried meconium contains about 85 to 95 per cent. of epithelium and mucus, almost all of which must be referred to this source. While, as regards its physiological import, it is impossible to doubt that it is (κατ' ἐξοχήν) the *excrement*:— that it is, in fact, the chief excretory ingredient of the fæces; and hence that ingredient, the dismissal of which from the intestinal canal is most essential to the welfare of the organism generally.

The above view, as to the share which both the biliary and the intestinal constituents take in producing the colour and odour of the fæces, appears so irrefragable, that we may content ourselves with a passing allusion to those experiments by which it has been attempted to establish the predominant or exclusive influence of either. Thus, while it has been pointed out by Valentin † that putrefying bile diffuses the strongest smell of ordure, Liebig ‡ states that he has succeeded in the artificial production of the fæcal odour by a process which essentially consists in imperfectly oxidizing some of the more azotized tissues of the body. The latter experiment has been regarded as leading to the inference, that

* Brown Séquard, "Experimental Researches in Physiology and Pathology," New York, 1853.

† See p. 366.

* The green colour of the stools after calomel has been taken seems to be due, partly to the chemical reaction of the contents of the intestine, partly to an increase in the quantity of bile poured out. The latter fact has been confirmed by experiments, in which this drug has been administered to dogs provided with biliary fistulæ opening externally. The chemical change undergone by the mercury in the intestinal tube consists (like that of the salts of iron under similar circumstances) in the formation of a sulphuret of the metal.

† Lehrbuch der Physiologie, vol. i., p. 370.

‡ Animal Chemistry, 3rd ed., p. 148. *et seq.*

certain effete constituents of the blood are secreted into the intestine, in a like state of partial oxidation. But, even could we assume the chemical identity of two substances merely from their having the same overpowering smell, we should still be left in uncertainty, as to whether these odorous matters were excreted directly from the blood into the bowel, or were introduced into it indirectly, by means of the secretion and subsequent metamorphosis of the bile. The very large intestinal constituent of the meconium, associated as it is with an almost inodorous character of this excrement, would indicate that, on the whole, Valentin's view of the biliary origin of the fæcal odour is the more correct one. At present, however, a satisfactory decision of the question seems impossible.

But whether the peculiar odour of the fæces be biliary or intestinal, there can be no doubt that it is derived, in the first instance, from the blood. For the smell of the excrement of any particular species always has a close relation to that odour, which is specific to the body of the animal, and which appears, in various degrees of intensity, in all its different excretions. And it is even stated by Wehsarg* to present differences specific to the individual.

Finally, we need have little scruple in asserting, that all the physical properties of the fæces are also in a great measure dependent on that alimentary residuum which usually enters so largely into their composition. The quantity of fatty matter and of casein usually present in the excrement of the sucking-child, the deepening (and finally black) colour of the fæces in persons who feed chiefly on vegetables, the lactic acid found in the evacuations of carnivora, or the oil which may often be detected in the stools of persons by whom even small doses of cod-liver oil are being taken medicinally — form instances of this kind, which might obviously be multiplied to almost any extent. Nor is the process always limited to a mere admixture or decomposition of the food itself. On the contrary, the metamorphoses which most of its ingredients have to undergo, often react on the secretory contents of the canal, so as to modify their appearances by the addition of properties more or less foreign to them. And nothing but that comparatively uniform admixture of the chief alimentary principles of the food, which we shall hereafter find is absolutely necessary to the life of the individual, will account for even the imperfect uniformity traceable in examining the excrements of large numbers of individuals.

The reaction of the human fæces is generally acid; sometimes neutral or alkaline. The quantity daily evacuated by a healthy male adult may be estimated as amounting, on an average to about five ounces avoirdupois.

The specific gravity of the fæces is generally greater than that of water, owing to the solids which they contain. But it is far too variable to allow of any average estimate being made. For it varies, not merely with the bulk and weight of the alimentary residue that forms so large a portion of the ordinary excrement, but also with the degree in which the fæcal mass has been condensed by the absorption of its watery constituents. And it would further seem, that the fæces are capable of being partially dried, and rendered much lighter, by a mechanical admixture of intestinal gases with their substance while still within the body. At least it is very common for different portions of the same evacuation to exhibit very different specific gravities: — the first portions of the excrement, which previously occupied the lower extremity of the rectum, being much lighter than water; while those subsequently extruded, though less solid, are so much heavier, as to sink rapidly in this liquid.

The mechanical composition of the excrement might almost be deduced from what has already been said of its origin. A large quantity of its mass no doubt consists of undigested food.* This must, however, be subdivided into two parts, which have a very different import with respect to the digestive function. One of these, which is usually much the larger, includes all those substances that are incapable of being dissolved by the various secretions poured into the intestinal canal. Such are the harder parts of various animal and vegetable tissues: — the sarcolemma of muscular substance, the cells of cartilage, fragments of bone, the elastic fibres of areolar tissue; together with the husks, shells, pods, chlorophyll, epidermis, and various dense membranes, cells, vessels, and fibres of the various fruits and seeds used as food. Some of these tissues quite defend the soluble contents they enclose. The other portion consists of substances which, though really capable of solution in the alimentary canal, have escaped this process: — whether from having been taken in too large a quantity, from not having sojourned in the tube during a sufficient interval of time, or from having been exposed to secretions which are partially devoid of their proper solvent force. Of these three causes of such an admixture, the first is the more common, and probably constitutes an invaluable safeguard against the dangerous results which might otherwise follow every act of over-eating. Hence in the state of repletion, whether relative or absolute, large quantities of fat, muscular fibre, albumen, casein, starch cells, fibrous tissue, and other strictly alimentary substances, escape digestion, and are found in the fæces. And conversely, it is highly probable that individuals (as well as animals) may have their digestive powers so raised by

* Microscopische und Chemische Untersuchungen der Fæces gesunder Menschen. Giessen, 1853.

* The analyses of Wehsarg assign to the dried substance of this constituent an amount which would probably be equivalent to a proportion of about 13 per cent. of the whole excrement. But we may suspect this to be rather too low an estimate; and are at any rate justified in doubting whether the alimentary ingredient could be completely isolated, for the purpose of being thus determined.

hunger and need, as to be enabled to extract nutriment from substances that would otherwise defy the action of their gastric and intestinal juices. In short, these undissolved and insoluble—undigested and indigestible—constituents of the alimentary residuum may almost be said to merge into each other, according to the habits of the individual with respect to the ingestion of food.

That element of the fæces which is derived from the digestive organs of the animal itself, consists chiefly of mucus and precipitated bile. This mucus is, for the most part, structureless; but is mixed with variable quantities of scaly epithelium from the rectum in the neighbourhood of the anus. In violent diarrhœa, columnar cells from the intestine may also be found in the evacuations :—sometimes in the younger cell-form of abortive cytoblasts or nuclei, sometimes in the more advanced state of simple ovoid cells. The latter are sometimes met with in small numbers, even in healthy fæces; and constitute what are often termed mucus-corpuscles. The biliary constituent is found chiefly in the form of minute amorphous masses or molecules of a resinous character; crystals or plates of cholestearine; and soluble colouring matter, that often stains the cells just mentioned, as well as the other mechanical constituents of the excrement.

The crystals of ammoniaco-phosphate of magnesia, which are so often found in the fæces, can hardly be definitely allotted to either of the two foregoing sources. They are easily recognised by their characteristic shape. They were formerly supposed to be peculiar to the stools of diarrhœa and typhus. But they are found in the healthiest fæces. Their occurrence appears to be favoured by all circumstances which further decomposition. They are therefore probably due to the action of ammonia (developed in the fæces before or after their expulsion) upon that neutral phosphate of magnesia, which we shall see forms so large a proportion of the entire saline constituent of the excrement.

The chemical composition of the fæces will of course exactly correspond with the nature and amount of those substances of which it forms the mechanical admixture. Hence, not only is it impossible to lay down any average that can apply to fæces generally, but it is even probable, that no two specimens of excrement are composed of the same proximate constituents mingled in the same proportions.

Berzelius* analyzed the fæces of a labourer who had fed on coarse, hard-baked bread, with moderate quantities of meat and vegetables. He obtained the following results:—

Water			75·3
Substances soluble in water	Bile	·9	5·7
	Albumen	·9	
	Extractive	2·7	
	Salts	1·2	
Insoluble residuum of the food			7·0
Insoluble substances added in the intestinal canal: mucus, biliary resin, fat, and sundry animal matters			14·0
			102·0

* Lehrbuch der Chemie. Bd. ix. p. 341.

Without, however, impugning the accuracy of an analysis conducted by such an eminent chemist as Berzelius, it seems important to point out that, for physiological purposes, it is all but useless. For not only does it afford no inference as to the quantitative composition of the fæces generally, but it even suggests grave doubts as to the correctness with which its own chief results have been grouped together. Recalling, for example, our subdivision of the constituents of the fæces into alimentary and secretory, we inquire in vain how much of the soluble albumen and extractive of this analysis was derived from the food, and how much may be ascribed to the secretions poured into the canal. In like manner we are ignorant whether its fatty constituent was not partly the undigested residue of fat which had been introduced with the food. But from a comparison of this analysis with some observations on the meconium by Hoefle* and Lehmann †, we may conjecture, that while the protein compounds found in healthy excrement belong almost exclusively to the food, a small quantity of its elain and margain, and a larger amount of its muco-gelatinous extractive, are derived from the secretions of the animal itself.

The inorganic constituents of the excrement must also vary greatly with the nature and amount of its alimentary residuum. Porter‡ states that healthy fæces, when dried, contain on an average about 6·7 parts per cent. of mineral substances. Wehsarg reckons these salts at 4·1 per cent., from an average of seven analyses. But an analysis by Dr. Percy§ estimates them at 16·4 per cent. This proportion somewhat approaches that given in the analysis by Berzelius quoted above. It also corresponds with some analyses by Macaire and Marcet ‖ of the fæces of the Dog and Horse, which they found to contain 20 and 25 per cent. of ash respectively.¶ The soluble salts form between one-fourth and one-third of the whole ash. The phosphates of the earths and alkalies constitute about one-third of all the salts present. While the chlorides of the alkalies are reduced to the very small proportion of about one-thirtieth; a proportion which is about equalled by the whole of the sulphates. The chief remaining peculiarities worthy of notice are, that the quantity of potash is from 10 to 40 times greater than that of the soda; and that the magnesia reaches half the amount of the lime. Of these two quantitative disproportions, the first seems due to the food; while the latter has been referred by Berzelius to the more active

* Chemie und Mikroskop am Krankenbette, p. 85.

† *Op. cit.*, vol. ii. p. 135.

‡ Annalen der Chemie und Pharmacie, bd. lxxi. p. 109.

§ Day's Simon's Chemistry, vol. ii. p. 375.

‖ Société d'Histoire Naturelle de Genève, vol. v. p. 230.

¶ This difference, like that of the nitrogen of the excrement in these animals (4·2 per cent. in the Dog to ·8 in the Horse), probably depended on the contrast between the animal and vegetable nature of their food.

absorption of lime than magnesia in the intestinal canal. Carbonates of the alkalies are found in the ash of human excrement; but they are apparently almost absent from that of the Sheep, Cow, and Horse. They are probably produced by a combustion of some organic salts of these bases.

The elementary analyses of the fæces hitherto made possess little physiological significance, or general validity. But from what has already been stated, it is obvious that the entire excretory part of the ordure removes from the body very little water or nitrogen;—probably not more than $\frac{1}{30}$th or $\frac{1}{40}$th of that quantity of each of these elements which is daily excreted in the urine.

The time during which the contents of the intestinal tube sojourn in its different segments is probably a very uncertain as well as variable one. In diarrhœa, the whole canal is sometimes traversed by these contents in two hours; while in obstruction, weeks or months may elapse without their complete transit. The mean rate which lies between these two morbid states can only be conjectured. But there are reasons for supposing, that the food of a healthy adult occupies about twelve hours in passing through the small intestine. While from thirty-six to sixty hours may be assumed as its average sojourn in the large intestine, prior to its ultimate expulsion from the rectum.

Intestinal gases.— In speaking of the elastic fluids which are generally contained in the large intestine, and are occasionally expelled from its lower orifice, it will be advantageous to contrast them with the gases found in other parts of the alimentary canal: — viz., in the stomach and the small intestine. Many years ago the composition of these gaseous contents of the canal was correctly given by Jurine, from an examination of the corpse of an idiot soon after death by cold. But it is to Magendie* and Chevreul that we owe the only trustworthy quantitative analyses on the subject. Their observations were made upon the gases found in the bodies of criminals immediately after their execution. Some authors have therefore thought it worth while to allude to their results, as being probably affected by the dyspepsia which the dread of such an impending doom might be supposed to have produced in these unhappy persons. Without, however, assigning any definite value to this contingency, it is enough to say that they still remain far preferable to any other such analyses:—to those, for instance, of Chevillot†, whose rather different results are quite explained by the time after death to which his examinations were deferred, and the decomposition which had therefore begun, both in the tissues of these corpses, and in the alimentary and secretory contents of their intestines.

We may best arrange these analyses in the following tabulated form: —

Whence obtained.	Composition by Volume.					
	Oxygen.	Nitrogen.	Carbonic Acid.	Hydrogen.	Carburetted Hydrogen.	Sulphuretted Hydrogen.
Stomach - - - - -	11·00	71·45	14·00	3·55	- -	- -
Small intestine: average of three analyses - - - -	- -	31·84	29·80	38·36	- -	- -
Cœcum - - - - -	- -	67·50	12·50	7·50	12·50	traces.
Large intestine 1. - - -	- -	51·03	43·50	- -	5·47	traces.
Large intestine 2. - - -	- -	18·04	70·00	11·06	11·06	- -
Rectum - - - - -	- -	45·96	42·86	- -	11·18	traces.
Flatus expelled *per anum* (mean of two analyses by Marchand) -	- -	21·5	40·5	18·75	18·75	·5

It is only from such analyses that we can form any reasonable inference as to the origin of the gases to which they refer.

In making such an inquiry, four sources of aëriform matter at once suggest themselves; either of which seems at first sight capable of at least partially explaining the presence of gaseous substances in the digestive canal. And the claims of each of these must be separately examined before we can conjecture the probable amount of its product, or its share in those reactions which the physical properties of gaseous fluids so easily allow them to excite.

1. Air may be introduced into the intestinal canal from without the body. Just as some of the lower animals can distend the abdomen by a voluntary deglutition of air, while even the higher Mammalia have been noticed to fill the stomach with air by the movements which precede the act of vomiting, so persons have been observed to swallow air, and afterwards expel it by eructation. And apart from such exceptional cases, there is good reason for believing that the ingestion of food always introduces into the stomach an appreciable quantity of atmospheric air; part of which is perhaps mechanically carried down with the alimentary bolus, while another part enters the organ in a state of more minute division, with the frothy saliva.

The air which is thus introduced into the stomach will doubtless here undergo a certain amount of diffusion or interchange with the elastic fluids dissolved in the liquid blood that

* Précis Elémentaire de Physiologie, vol. ii., p. 113.

† Chevillot's figures (Berzelius' Jahresbericht der physischen Wissenschaften, 1831, p. 247) indicate that, in the diseased and decomposing bodies he examined, oxygen was always present; and carbonic acid rather increased; while the nitrogen sometimes reached the large proportion of 99 per cent.

circulates in the capillaries of the organ. And this diffusion probably imitates that which takes place between the air and the blood at the surface of the lungs and skin. It will therefore convert the gaseous mixture of the atmosphere into one containing less oxygen, and more carbonic acid; the extent of the change in both these respects varying chiefly with the duration of its sojourn in the stomach.

But a number of circumstances unite to prove that the gases of the stomach are in great part derived from some other source. Thus the quantity of air taken with the food can be but small. While percussion and auscultation show, that the cavity of the healthy organ is often largely distended with gas. And the above analysis further points out, that not only is the increase of carbonic acid disproportionate to the decrease of oxygen, and therefore (unlike the interchange in the skin and lungs) not due to a mere physical process of diffusion, but that a new element, hydrogen, has been added to it.

The same arguments apply still more forcibly to those gases, which almost invariably distend the intestines. For during digestion, they could hardly pass the pylorus; and at any other time, would be very unlikely to enter the stomach, through which alone they could reach the duodenum. Hence in the case of the intestinal segments of the canal, we are referred almost exclusively to those sources which, we have already seen, will be necessary to explain the greater part of the gas present in the stomach.

2. Gases may be developed in the alimentary canal from the decomposition of the food which it contains.

Difficult as it is to decide on the evidence at present before us, there seem to be valid reasons for regarding this as the process by which the intestinal gases are chiefly, if not exclusively, set free in the alimentary cavity. The food introduced into this cavity is speedily converted into a decomposing mass, which is useful to the organism solely by virtue of the metamorphoses it is undergoing. And though these metamorphoses generally seem to be limited to processes, by which elements are merely re-arranged in the solid or liquid form, and not given off as gases, still they are easily susceptible of being carried further, so as to involve a more or less copious evolution of gaseous fluids.

Now, the putrefaction of the protein compounds of the food, together with the fermentation of its hydrates of carbon, would amply account for these gases; as well as for the ammonia which has been alluded to as probably throwing down part of the soluble phosphates of the intestinal contents, in the form of crystals of the triple phosphate of ammonia and magnesia. For not only are all the gases in the above analyses producible by the various processes of putrefaction external to the body, but their proportions to each other are precisely those which might be expected from the known composition of the food.

The conditions which favour the presence of these gases remarkably confirm this view. Too large a quantity of food—and especially of food that consists of substances which are either putrefying or fermenting, or are peculiarly liable to undergo these changes—notoriously increases the amount of gases thus generated in the bowels. The liability of cattle to a dangerous distention of this kind, when surfeited with green food, is well known to agriculturists. And in like manner, an increased quantity of sulphuretted hydrogen is generally expelled in the flatus of animals which have been fed upon* beans, or made to take sulphur with their food. While the practice of medicine acquaints us with the fact, that all circumstances which lower the tone of the alimentary canal, or lessen the energy of its secretions, further these spontaneous (though abnormal), metamorphoses of its contents; and thus give rise to a corresponding increase in the quantity of the gases which form their direct result. We may perhaps find an additional confirmation of this view in a comparison of the various instances analyzed above. At least, the great deviations which they exhibit, seem better explicable by the variable composition of the food, than by any theory which would refer their development to the organism or the blood itself.

Finally, it is well known that the complete exclusion of food from the digestive cavity often gives rise to a peculiar white and contracted state of the tube, which implies an entire absence of all such gaseous contents from the greater part of its length. This appearance is so generally seen in the bodies of animals after long fasting, as to constitute an important feature in the medico-legal evidence of death by starvation.

3. It has been supposed that gases are set free in the intestinal canal by a kind of secretion or transpiration from the blood.

But in alluding such a process, it is necessary to premise that, strictly speaking, it would hardly deserve the name of a secretory act. Even assuming that it really discharged the gases of the blood into the intestinal canal, we should scarcely be warranted in terming their passage a true process of secretion. On the contrary, all analogy indicates that it would rather constitute an act of diffusion:—a diffusion which would probably obey the same laws, and exhibit somewhat of the same course, as that which chemistry has successfully investigated in the case of the lungs and skin.

In any case, unless we suppose the capillaries of the intestine to be the actual site of an unexampled generation of gas from the constituents of the blood, an inquiry into these latter will probably afford us some grounds on which to accept or reject the above theory.

It is therefore important to point out, that some of the gases found in these analyses—viz. hydrogen, carburetted hydrogen, and sul-

* The legumen of which contains much of this element.

phuretted hydrogen — have never yet been detected in any appreciable quantity in the blood. And hence without assuming their complete absence from this liquid, we may at least infer that they are not present in that amount which would be necessary to explain their secretion from it, to the extent mentioned in these observations.

To this we may add, that no parallel to such a process of gaseous excretion can be observed in the case of any other vascular surface. This statement not only holds good of the serous membranes, but (what is much more conclusive) even of those structures which are specially organized with reference to the giving out from the blood of certain of its gases, and the taking up of others from the surrounding air. It is to the skin and lungs that we should naturally look for evidence of the true secretion of excrementitious or noxious gases from the circulating fluid. And yet, on turning to the results afforded by the eudiometric researches of a number of observers, we find that the gases which we have just stated to be absent from the blood, are equally deficient in the air exhaled from the vessels of these special organs of gaseous excretion. While even the carbonic acid and nitrogen of the intestinal flatus are at once distinguished, by their quantitative relations, from the same gases, as found in the air of expiration. Thus the minute amount of nitrogen in the air exhaled from the lungs is contrasted with an average of 40 per cent. in the gases contained in the intestines; and its proportion to the carbonic acid present, is increased from $\frac{1}{100}$th in the former, to $\frac{1}{3}$d, or even $\frac{2}{5}$ths, in the latter gaseous mixture.

In conclusion, we may point out, that while the carburetted and sulphuretted hydrogen, as well as the pure hydrogen, of these analyses, can only be explained as the result of a process which directly or indirectly involves the deoxidation of water, — the chemistry of the organism seems always to reverse this process. Far from deoxidating this liquid, there are good grounds for supposing that a quantity of water amounting to nearly $\frac{1}{5}$th of the whole aqueous contents of the food is daily formed in the body by a combustion (or in other words, by an oxidation) of the hydrogen of its tissues.

But some will perhaps think that these considerations are sufficiently answered by facts, which deserve more reliance than any such arguments.

They would possibly instance experiments like those made by Magendie * and Girardin, and confirmed by Frerichs †: in which the deligation of an empty portion of intestine had nevertheless been followed by its distention with flatus. Or they might call attention to the tympanites of typhus fever, and other kindred disorders, in which little food has been taken for a long period of time. But a little reflection might teach us that none of these instances have absolutely excluded the presence of all alimentary substances; and that a very small quantity of liquid or solid matter would probably be quite sufficient to yield the gases observed.

4. Lastly, as regards the intestinal gases present in diseased subjects, we may conjecture a fourth source of such elastic fluids:— namely, the decomposition of the various secretions of the canal. For it is not too much to assume, that the decomposition to which the alimentary contents of the intestine appear to be often exposed, is sometimes shared by the secretions poured into its* cavity; especially when we recollect that, in many diseases, the state of all the fluids of the organism is frequently such as notoriously favours the access of putrefaction in the tissues after death.

The gases expelled from the large intestine carry with them the odorous principles of the excrement. It is, indeed, probable that they become impregnated with these volatile substances mechanically, as a necessary result of their contact with them in the bowels. But reasons are not wanting for the conjecture, that the introduction of certain fœtid substances into the blood, is subsequently followed by their specific determination to the mucous membrane of the intestinal canal; which thus forms a channel for their elimination from the system. For after the inhalation of any particularly offensive odour, the fæces and flatus often exhibit what is unmistakeably the same smell, in a very concentrated form. And the active diarrhœa which frequently attends this reproduction of the odour, seems a part of the same effort of nature, towards the removal of what other evidence, beside that of our senses, thus testifies to be an active poison.

Respecting the laws which regulate the forcible expulsion of these gases from the stomach or intestines, little need here be said. Though greatly influenced by habit, still the act is essentially voluntary. Its mechanism is so closely akin to that of defæcation as not to require any separate notice. Whether the immediate stimulus to this expulsive act is always mere intestinal distention, or whether it is sometimes determined by the quality (as well as quantity) of the elastic fluids, cannot at present be decided.

We are equally ignorant as to how far, failing such an expulsion, these gases are capable of being absorbed into the blood; and if so, where they emerge from the vascular system, or what form they assume in doing so. The small quantity of sulphuretted hydrogen really present in the most offensive flatus, and the comparative harmlessness of carburetted hydrogen in the proportions in which it would be dissolved by the blood, prohibit us from coming to any conclusion based on the ordinary physiological action of these two gases. We can but conjecture, that whatever absorption they may undergo is slow enough

* Recherches physiologiques sur les gaz intestinaux. 1824.

† *Op. cit.*, p. 866.

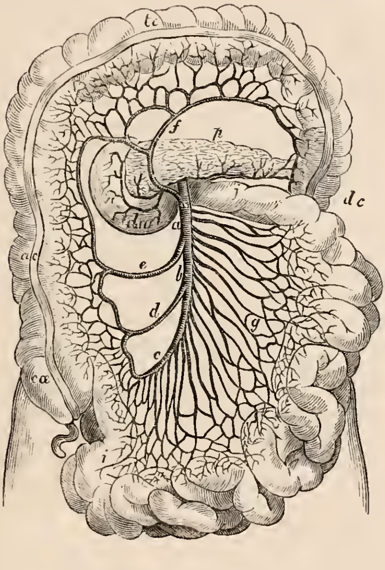
* The cases of physometra adduced by obstetric authors seem to be examples of a similar decomposition occurring in the blood and secretions contained in the cavity of the uterus.

to allow of the much quicker destruction of their poisonous properties by a more or less perfect oxidation.

Arteries of the intestines.—We have seen that the stomach and duodenum are supplied with arterial blood by means of various twigs derived from the three branches of the cœliac axis, which springs from the upper part of the abdominal aorta. The remainder of the intestinal canal is furnished with arteries which are given off by two large branches of the abdominal aorta. These branches are named, from their position and distribution, the superior and the inferior mesenteric.

The *superior mesenteric* artery (*a, fig.* 277.), the longer of these two branches, is distributed over that large segment of the intestine which is formed by the lower part of the duodenum, the whole of the jejunum, ileum, and cœcum, and the first two-thirds of the colon. The

Fig. 277.



Distribution of the superior mesenteric artery to the small and large intestine.

a, trunk of the superior mesenteric artery; *b*, ileo-colic artery; *c*, its iliac branch; *d*, its colic branch; *e*, right colic artery; *f*, middle colic artery; *g*, arches formed by the anastomosis of the branches to the small intestine; *p*, pancreas; *du*, duodenum; *j*, jejunum; *i*, ileum; *c æ*, cæcum; *a c*, ascending colon; *t c*, transverse colon; *d c*, descending colon.

trunk of the vessel comes off from the aorta, at a point which about corresponds to the upper border of the second lumbar vertebra. It is separated from the cœliac axis by the pancreas; and hence is distant about a third of an inch from the origin of the latter vessel. From this commencement, it passes downwards and forwards, crossing over the termination of the duodenum, so as to reach the upper part of the mesentery. It now continues downwards between the two layers of this fold of peritoneum, which it occupies near its attachment to the posterior wall of the abdomen. Hence its length and direction correspond to those of the attached border of the mesentery itself; and are such, as to conduct it downwards and obliquely towards the left side, to a termination that corresponds to the end of the ileum, or the commencement of the cœcum. But the branches given off to these latter segments of the intestine by the trunk of the vessel are so large, and so directly continuous with its previous course, that it is only in a very arbitrary and limited sense that we can speak of it as ending in this situation.

The arrangement of the larger or primary branches of the superior mesenteric artery is liable to great variation, but is generally as follows.

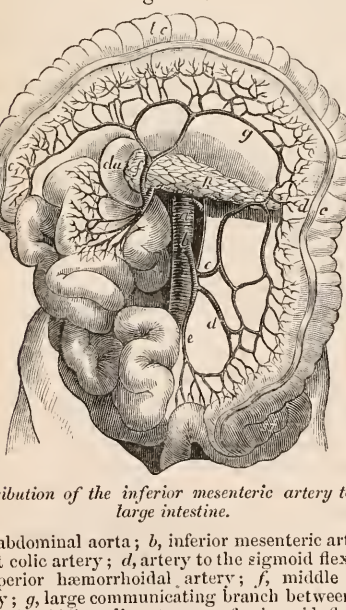
The trunk of the superior mesenteric artery is directly continuous with a large vessel (*b*, *fig.* 277.), which, when it has reached a distance of about two inches from the cœcum, divides into two others; of these the upper (*d*, *fig.* 277.) passes towards the cœcum, and the lower (*c*, *fig.* 277.) towards the ileum. The *ileo-colic* artery (*b*, *fig.* 277.), as the common trunk is named prior to its bifurcation, usually gives off from its right side one of rather smaller size, about three inches from the border of the bowel. The latter, which is called the *arteria colica dextra*, or right colic artery (*e*, *fig.* 277.), often arises by a separate trunk from the superior mesenteric. It takes a course almost horizontally outwards, or towards the right side, lying underneath the single layer of peritoneum which covers in the ascending colon, so as to reach this part of the large intestine at or near the middle of its height. Finally, at a distance of little more than an inch from its entering the mesentery, the trunk of the superior mesenteric artery gives off a large branch, the *arteria colica media* (*f*, *fig.* 277.), which passes upwards and backwards, enters between the two layers of the transverse meso-colon, and is distributed to the transverse colon, which it reaches at the middle of its posterior border. Besides these named branches, the superior mesenteric gives off numerous arteries (at *g*, *fig.* 277.), of almost equal size, which have not received any special designation. These twenty or thirty branches leave the left side of the artery, at various points between the lower border of the duodenum and the origin of the ileo-colic artery; and pass outwards, or to the left side, towards their distribution on the small intestine.

The further course of all these branches towards the small and large intestine affords a remarkable instance of an arterial anastomosis; such as is almost unparalleled in the whole of the body for the freedom and frequency of its communications, and the size of the vessels by which they are effected. Each of the primary branches just alluded to bifurcates: and its two resulting branches unite with those above and below them, so as to form a set (*g*, *fig.* 277.) of arterial arches; from the convexity of which spring new trunks, to divide and inosculate in a similar manner. This arrangement, which prevails throughout all the mesenteric branches that supply the intestine, is carried to such an extent in the jejunum and ileum, as to offer, in many parts, four or five successive sets of arches; which become smaller and more numerous as they approach the bowel, and finally give off the minute arterial ramifications that enter and traverse the intestinal coats.

On reaching the intestine itself, the greatly diminished arteries break up into still smaller capillary branches. These inosculate freely with each other, by comparatively large branches of communication; and thus unite and anastomose to form a dense stratum or flattened network of vessels, which occupies the layer of loose areolar tissue that separates the muscular from the mucous coat. This vascular plexus gives off, on the one hand, the vessels of the mucous membrane; and on the other, the not very numerous branches which run between and amongst the unstriped bundles of the muscular coat.

The *inferior mesenteric artery* (*b*, *fig.* 278.), which supplies the descending and sigmoid portions of the colon, and the whole of the rectum, is also a branch from the aorta. It arises from the front and left side of this vessel (*a*, *fig.* 278.), about an inch below the place where it gives off the left renal artery, and nearly the same distance above its bifurcation into the two iliac vessels. From this origin it is directed downwards and slightly outwards, lying successively on the aorta, the left psoas muscle, and the left

Fig. 278.*



Distribution of the inferior mesenteric artery to the large intestine.

a, abdominal aorta; *b*, inferior mesenteric artery; *c*, left colic artery; *d*, artery to the sigmoid flexure; *e*, superior hæmorrhoidal artery; *f*, middle colic artery; *g*, large communicating branch between the left and middle colic artery. *s f*, sigmoid flexure of the colon; *r*, rectum. (*t c*, *a c*, *p*, *du*, as in *fig.* 279.)

* In several of the preceding microscopic figures, the artist has been indebted to Koelliker's beautiful woodcuts for some details, which require this specific acknowledgment.

common iliac artery. During this part of its course, it lies at some distance from the intestine. But below where it crosses the common iliac vessels, it occupies the double fold of peritoneum (*meso-rectum*) that attaches the rectum to the pelvis. This terminal portion of the vessel, which is called the *superior hæmorrhoidal artery* (*e*, *fig.* 278.), is continued to a point about opposite to the middle of the sacrum; where it ends by bifurcating into two branches, which ramify on the opposite sides of the bowel, and are distributed to its various coats. These branches inosculate freely with the ramifications of the *middle hæmorrhoidal artery*, which is itself given off to the rectum by the internal iliac artery, or some of its branches.

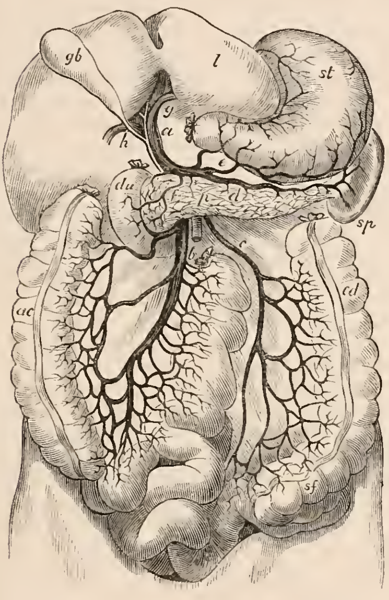
The only named branches of the inferior mesenteric are the left colic or *arteria colica sinistra* (*c*, *fig.* 278.), and the artery to the sigmoid flexure (*d*, *fig.* 278.). The former of these two vessels passes upwards and outwards, across the psoas muscle and left kidney, to reach the descending colon at about the middle of its height. The latter, which is sometimes double, also crosses the psoas, to enter the short meso-colon which attaches the sigmoid flexure of the bowel. The further distribution of both these arteries precisely recalls that of the similar colic branches from the superior mesenteric: each bifurcating into two branches; which, by uniting with the similar trunks above and below, form the origin of a set of arches that ramify in a second and third series. And as the union of the upper twig of the colica sinistra with the lower or left branch of the colica media unites the superior and inferior mesenteric arteries by a large anastomosing vessel (*g*, *fig.* 278.), all the arches of both these trunks have the most complete anastomosis with each other. So that it would be easy to trace out a continuous arterial channel of large size; which begins as the superior mesenteric, and passes through the ileo-colic, left colic, median colic, and sigmoid branches, to end in the superior hæmorrhoidal artery.

Veins of the intestines.—The veins of the intestinal canal are chiefly characterized by the fact, that the trunks formed by their convergence and union do not open into the right auricle, like the veins of the body generally; but undergo a second ramification and distribution, in their course from the capillaries of the intestine to the right side of the heart. This arrangement of course influences their distribution at two successive stages of their course. In the first place, their larger trunks fail to exhibit that close correspondence with the arterial channels which is seen in the case of most other parts of the body. And, secondly, instead of seeking the large vessels on the spine, these trunks converge into a single channel, the portal vein (*a*, *fig.* 279.), which passes upwards to the liver at some distance from the aorta and primary intestinal branches *

* See Art. VENOUS SYSTEM.

The veins of the intestines commence by a dense network, that receives the minute venous radicles into which the capillaries of the mucous and muscular coats return their blood. This plexus has the same submucous situation, and flattened shape, as the corresponding arterial network already mentioned; but, like the venous system in general, is composed of more numerous and larger branches. It gives off a number of veins; which leave the intestine, and gradually unite into the vessels that converge to form the various trunks. These branches have a tolerable correspondence with the primary ramifications of the arteries from the cœliac axis and the two mesenteric vessels. Many of

Fig. 279.



Branches of the portal vein.

a, trunk of the portal vein; *b*, superior mesenteric vein; *c*, inferior mesenteric vein; *d*, splenic vein, joined by the *e*, gastro-epiploic and pyloric veins; *f*, pancreatico-duodenal veins; *g*, branch of the portal trunk to the left lobe of the liver; *h*, similar branch to the right lobe.

(The remaining letters indicate as in the preceding figures.)

them unite to form two chief trunks, the superior and the inferior mesenteric veins. While others open directly into the splenic vein; or into the *vena portæ*, which is formed by the junction of it and these mesenteric veins.

The *superior mesenteric vein* (*b*, *fig.* 279.), which receives the venous blood from that portion of intestine supplied by the artery of the same name, travels for some distance in company with the latter vessel; lying on its right side, and somewhat superficially to it, and surrounded by very numerous lacteals and nerves. But near the lower border of the third portion of the duodenum, it swerves towards the right side, from what was hitherto an almost vertical course upwards; and after crossing in front of the duodenum at nearly a right angle, ends by joining the splenic vein behind the pancreas. This junction gives rise to the portal trunk (*a*, *fig.* 279.).

The *inferior mesenteric vein* (*c*, *fig.* 279.), — the origin of which also corresponds to the region supplied by the artery of the same name — generally commences as a single trunk at or near the border of the pelvis. From hence it ascends almost vertically, but with a slight inclination inwards, beneath the peritoneum, and on the psoas muscle; until, finally, it crosses under the transverse meso-colon, to end by a junction with the splenic vein (*d*, *fig.* 279.). In the latter part of this ascent, it is of course unaccompanied by the inferior mesenteric artery: and even below where this vessel is given off from the aorta, the artery and vein diverge so as to be comparatively distant from each other. Its junction with the splenic vein (*d*, *fig.* 279.), is usually about one or two inches from the point where this meets with the superior mesenteric vein. But it occasionally approaches much more closely to the latter vessel, or even joins with it prior to its union with the splenic to form the portal vein.

The branches of both these mesenteric veins resemble those of the corresponding arteries in their number and size, and in the remarkable freedom of their anastomosis. And this copious and frequent inosculation, — which coincides with an absence of all valves, — not only holds good of the several primary branches which converge into the portal vein, but also applies in some degree to those smaller ramifications, by which the portal system inosculates with the general venous system at the two extremities of the alimentary tube. Thus many of the smaller veins at the lower part of the œsophagus communicate with both the azygos and portal veins. While the lowest branches of the inferior mesenteric vein establish a similar and much more extensive anastomosis of the two systems, by their junction with a dense venous network — the *hæmorrhoidal plexus* — which encircles the lower part of the rectum, and gives origin to the middle and inferior hœmorrhoidal branches of the internal and external iliac veins.

The foregoing peculiarities in the vascular arrangements of the human alimentary canal are at present only susceptible of a very imperfect explanation.

As regards the arteries, their great number and size, and their large anastomosing channels, would probably be attended by several advantages. The variety of these channels would concede to the circulation, not only a large supply of blood, but one such as no ordinary local accident could at all interfere with.* The muscular fibre contained in their walls would allow these numerous tubes to exercise an unusual control over the amount of blood

* Compare the remarks on the vessels of the stomach at p. 327.

they from time to time convey. While on very simple hydraulic principles, these repeated cross branches would so diminish the various resistances (of impact and adhesion) offered to the blood within the vessels, as to permit, either a greater rapidity of the current, and hence a more rapid renewal of the mass of blood contained in the capillaries; or a more forcible pressure upon the latter fluid; or even both of these effects simultaneously.

It is perhaps a corroboration of the above conjectures, to trace their close relation to those which might be gathered from an independent consideration of the circumstances of the portal system. The trunk vein of this set of vessels leads to a second set of capillaries in the liver; through which there is nothing to propel the portal blood, save the force of the heart, aided by a small amount of suction, which the thorax exerts as it expands during inspiration. And hence, however large a quantity of the original cardiac pressure may be again amassed by the convergence of the various intestinal veins, still there can be no doubt that at least so much of it will have been lost, as to require all the aid which the above disposition of the arteries can afford it. But in spite of all such assistance, it seems probable, that the current of the portal blood is both far slower, and much more feeble, than that which occupies any of the arteries. Still it is no doubt quite sufficient for the exigencies of the circulation in the liver; and especially for that secretion of bile, to which the various details of the organization of this gland chiefly refer.

The Food. — The function of digestion has for its chief object the replacement of that loss of substance which the body is constantly undergoing.

Even the hardest materials of the globe we inhabit experience a gradual disintegration; as the result of the various physical processes to which they are exposed. Such processes may be instanced in the attrition and solution of solids, the evaporation of liquids, and the diffusion of gases. And hence, when we turn from these inorganic substances to the animal fabric; and consider its slight cohesion, the friction which its locomotion implies, its large watery constituent, and the feeble chemical affinities which enchain its elementary atoms — we shall scarcely be surprised to find, that the rapidity of its waste far exceeds that of the inanimate solids around us.

But the rate of waste, and the consequent need of replacement, both depend, far less on simple physical causes of this kind, than on certain actions which are specific to the organized body. These actions, which, in the aggregate, make up what we term Life, do not so much imply, as actually consist in, a perpetual process of flux and metamorphosis. This multiform change engages the whole of the corporeal tissues; and conducts their various ingredients, through a number of successive phases of composition, to an effete and useless state, in which they are finally ejected from the organism.

And hence, whatever the share taken by the physical actions of diffusion, solution, friction, and evaporation, in the removal of the substance of the body, they are not in any sense the true causes of its process of waste; or the real sources of its *egesta* or losses. They are but, as it were, the janitors of the animal fortress; the nature and amount of the matters which pass out by them being controlled and regulated by the higher life that rules within.

The *ingesta*, which replace these *egesta*, and thus form the opposite extreme of nutritional life, are equally influenced by the general requirements of the animal. Excluding, for the present, all consideration of that preponderance of absorption which determines the growth of a young animal, or the converse excess of excretion which results in the decrease and decay of an old one; and limiting our attention to the mere maintenance of the adult body:—we shall find that it is the composition of its structures, and the rate of their wear and tear, that chiefly determine the kind of food it makes use of, and the quantity it consumes within a given space of time. While as regards the exact degree of this dependence, we shall further find that, here as elsewhere, the operations of organized nature are only limited by wide general principles; within which are apparently conceded great variety and fluctuation. The laws of nutrition are, so to speak, universal in their range, but elastic in their application.

In respect to the *nature* of the food, we may first notice, that by far the larger part of it is always derived from the organic, and never from the inorganic, world. In other words, the chemistry of the organism has little power of construction or synthesis. So that, although a proximate analysis of the tissues of the animal body presents us with compounds, which may be shown to consist chiefly of a few elementary substances united to each other in varying proportions, still the carbon, oxygen, hydrogen, and nitrogen, which surround or penetrate the living animal, are never directly built up into these tissues. On the contrary, the various substances which form the proximate principles of the several structures of the organism are themselves produced by the metamorphosis of kindred compounds introduced in the food; — compounds which have been in their turn derived from the vegetable kingdom; either directly, in the shape of plants, or indirectly, from substances constructed out of vegetable tissues by the organism of another animal. And the inorganic substances introduced into the body seem to be almost restricted to the subordinate (though equally indispensable) office, of combining with these products of vegetable life, and modifying their actions in obedience to the necessities of the existing individual.

The above statement as to the organic nature of the food suggests some interesting considerations.

In the first place, it seems to shew that the living animal of to-day pre-supposes another organization of yesterday ; — that its individual descent from two creatures of the same species is accompanied by a less evident, but quite as real, transmission of substance from several previous beings. In short, that the greater part of its entire mass might be regarded as the sum of various legacies, which have been bequeathed to the existing organism by the various plants and animals that lived before it.

In the next place, it indicates a fixed and definite relation between the plant and the animal. The former is thus the chief agent in the constructive chemistry of the latter :— a necessary link in that chain of processes which builds up organic principles, out of the elements of inorganic nature, or out of those simple products into which the particles of the animal body are finally converted by its waste during life, or its putrefaction after death. The carbonic acid given off by the living or dead animal may especially exemplify the latter remark ; converted as it is, by the vegetable, from a poisonous gas into a class of substances which are in the highest sense alimentary, and essential to the life of the animal.

And lastly, since animal and vegetable life are thus complementary to each other, alike in their broader features and their minuter details, we may conjecture that, in the present disposition of our planet, they form what is in fact a tolerably constant magnitude : — a sum of organized life, the amount of which is subject to but very slight variation from one time to another. Nay more, we may almost suspect that the total of animal existence — the composition of which ranges thus regularly through vegetable organization as an essential part of its cycle of metamorphosis — is in the main equally constant and fixed. Created by what even modern science must be content to own as a miracle, in the strictest sense of the word, it seems not improbable that animal, as well as vegetable life, is sustained in consonance with some vast law of this kind. According to such a law, each by each, and both together, would make up certain constant units ; the innumerable constituent fractions of which might vary within vast limits without exercising any effect on their respective sums. And thus the world of life around us would but parallel that perpetual flux, but unaltered quantity, which the chemist has long predicated of the various materials which compose the inorganic globe we inhabit.

But if, on the one hand, the animal is incapable of constructing its complex tissues from the simple elements of inorganic nature, still, on the other hand, it is not bound down by such rigorous chemical necessities, as to demand a food possessing an exact identity of composition with itself. A large proportion of the animal creation feed on a vegetable diet, the constituents of which deviate considerably from those of their own mass. And but very few of even the more carnivorous animals are in the habit of devouring their own species. Finally, though the blood forms the pabulum of all the tissues, and hence closely approaches their total composition, still it does not appear to form even an advantageous article of food, far less an indispensable one.

And while such considerations may suffice to show, that there is no true identity between the food and the tissues in general, the progress of modern physiological chemistry plainly indicates, that an identity of this kind would be equally impossible in detail. Thus it is not improbable, that the tissues of every individual possess chemical peculiarities more or less specific to himself. And it is all but certain, that the various proximate principles isolated by the chemist are not definite combinations of certain elements in equivalent proportions — as are the salts, acids, and alkalies of the inorganic world — but rather ever-varying mixtures. Those various forms of protein which it is so convenient to distinguish by the names of albumen, fibrin, and casein, may indeed be separated from the tissues of animals, and even of vegetables, by the same rough processes ; and may therefore respectively exhibit the closest resemblance in their composition and properties. But an accurate analysis would probably show, that the organic substance represented by either of these terms is never precisely identical in any two specimens. It is the total of a number of constituents, the result of a variety of processes, the end of a serial metamorphosis : rather than a definite and specific compound of carbon, oxygen, hydrogen, and nitrogen.

And not only is there no identity in the composition of the organism and the ingesta, but it would seem that there are some tissues of the body which have absolutely no representative in the food : no kindred substance to which their formation can possibly be referred. Such are the various tissues that yield gelatine ; a substance which, though it appears to escape assimilation when introduced into the organism from without, is yet constantly formed within it, from the metamorphoses of other parts of its substance.

The chemistry of nutrition therefore implies neither construction, on the one hand, nor identity, on the other ; but something midway between these two extremes. Its forces occupy, so to speak, a debateable ground between the prehension of old materials, and the formation of new ones. And the food submitted to its action is only required to possess such a similarity of composition with the body, as will concede these limited changes, without implying any wider process of metamorphosis.

Any exact definition of the degree of resemblance thus requisite, would be foreign to our present object. Indeed, in the existing state of our knowledge, it is impossible to specify the precise nature of those metamorphoses, which accompany the digestive act, and are bounded by the food and the organism as their respective beginning and end. It is enough to indicate, that they appear to be intermediate between the forces of chemical affinity on the one hand, and homogeneous and heterogeneous adhesion on the other; and that while they are sometimes * akin to the formation of hydrates, they occasionally resemble those still more recondite phenomena which are concerned in the production of isomeric or isomorphous compounds :— substances which, though identical in their composition, offer striking differences in their solubility, as well as in many of their chemical properties and reactions.

This very limited convertibility of the main components of the food, renders their variety almost as essential, as though each different tissue of the body had required the entry of its corresponding substance from without. In other words, within the range of the chemical parallelism just mentioned, the organism demands alimentary compounds containing all the different ingredients necessary to cover its own waste.

This fact receives a good illustration from that selection which the instinct of most persons would impel them to make. Left to himself, Man always chuses a mixed diet, composed of proper quantities of animal and vegetable, liquid and solid, matter. Nay more, that almost equally imperious instinct which urges him to vary his diet, though often confused with the morbid cravings of luxury, is essentially nothing less than an expression of the natural wants of a healthy organism.

Obscured, however, as these really natural instincts often are by the stereotyped tastes and habits of a highly artificial state of society, we gain a far better insight into the proper composition of food, by examining that store of nutriment which, in the shape of the yolk of the Bird's egg, or the milk of the Mammal, Nature herself provides for the maintenance of the young of these classes. Of these two substances, the milk is justly regarded as forming the very best example of a proper food :—both as regards the nature of its several ingredients, and the proportions in which they are mingled with each other.

Milk.— The alimentary properties of the milk are due to the presence of a number of proximate constituents, the more important of which may be enumerated as follows. — (1) A protein-compound, casein; (2) a hydro-carbon or fat; (3) a hydrate of carbon or sugar; (4) certain salts; and (5) the water in which the whole of these materials are suspended or dissolved. Of these five groups of substances, at least four are indispensable ingredients of every proper food. The hydrate of carbon and the hydrocarbon are, to some extent, capable of forming substitutes for each other. But with this exception, (an explanation of which will be attempted by and by), the absence of any one of these constituents, or even its presence in insufficient quantity, suffices to destroy the capacity of any particular food for maintaining life; so that an animal limited to such a diet ultimately dies with appearances of inanition. And *à fortiori*, the ingestion of but one of these alimentary ingredients, — such as albumen, fat, or sugar, — is soon attended with effects which still more closely resemble those of starvation. Such a diet does indeed essentially starve the entire organism, even while it supplies some of the constituents of its lost substance. For although the unchecked waste of the remaining constituents of its mass tells upon certain of its textures with greater rapidity and energy than on others, still it ultimately involves the whole in a common destruction: — a fact which need little surprise us, when we recollect the mixed composition of the simplest tissues, and the intimate mutual dependence of the most distant and isolated parts.

Constituents of food.—1. The first group, consisting of what are called the protein-compounds, includes a number of proximate principles, which are derived from both the animal and vegetable kingdoms of nature. The chief of these principles are albumen, fibrin, and casein. By digestion in solution of potash, and precipitation with an acid, either of these yields a substance called *protein*: — a name that alludes to the relation this principle is supposed to bear to all the compounds from which it is thus obtained. It is regarded as their common starting-point (πρωτεύω, *primas partes teneo*), and most essential component. And the slight differences of composition offered by each particular protein-compound, are explained as chiefly due to variations in the nature and amount of certain collateral ingredients, the addition of which to protein imparts the specific characters of albumen, fibrin, or the like. Hence the various protein-compounds are supposed to differ, not so much in elementary composition, as in certain characters which might almost be termed morphological: — namely, outward form, physical properties, degree of solubility, and the like.

The exact process by which one of these protein-compounds undergoes conversion into another is still a complete mystery. But that such changes do constantly obtain, cannot be doubted. And hence, while the quantity of albumen in the animal body, and the constancy with which it is present, assign to this proximate principle the leading position in the above group of proteinous substances, it is on its generic, and not its specific, properties that our attention ought chiefly to be fixed.

The protein of the food may be regarded as its most essential constituent. The reason why such an importance is ascribed to it becomes sufficiently evident, when we compare its composition with that of the body which it is intended to nourish. The highly azotized constitution it possesses ($C\ 54{\cdot}7 + H\ 6{\cdot}8 + N\ 14{\cdot}2 + O\ 24{\cdot}3 = 100$) closely approaches that of the solids of the organism generally. And it shows an equally important relation to most of the tissues in detail. It forms a large constituent of the blood; and therefore of the plastic nutritional fluid that

* Compare the remarks on the gastric juice at p. 337.

exsudes directly from this fluid. It is the main component of the muscles, which execute the various movements of the body. It is an equally important ingredient in the tissues of both the central and peripheric parts of the nervous system. It is probably the source of the gelatinous * tissues; which, in herbivorous animals, can only be derived from a kind of degradation or regression of the albuminous substances. And, finally, its large amount in the structures of the fœtus proves that it is just as important to the evolution and growth of the animal, as it is to its maintenance. In short, in protein and its various kindred substances, we recognize the principle, which forms the material exponent of all the structures and functions, and is the chief substantive agent of the chemistry of life.

The quantity of protein necessary for the proper maintenance of the healthy animal can only be estimated from very indirect and approximate calculations.

In milk, the albuminous compounds are chiefly represented by casein, which forms about $3\frac{1}{2}$ per cent. of its total quantity. But we can scarcely guess how much milk is daily consumed by the sucking animal, or what proportion this amount bears to the weight of its whole body. And we are justified in assuming, that a large fraction of the protein thus introduced into the system, is applied to exigencies of growth and development which have little or no place in the adult animal.

Assuming an exact maintenance of the adult organism, without increase or decrease, we might expect that an examination of its various azotized excretions would teach us how much nitrogen had been discharged from the system within a given time: and hence that, by comparing this quantity with the known elementary composition of protein, we might be enabled to calculate how large a quantity of the azotized constituent of the food ought to be added to the system, in order to replace its daily loss.

But here we are met by a difficulty connected with the process of nutrition itself:—with that chain of events of which food and waste constitute only the extreme links. The amount of nitrogen given off by the body does not depend solely upon the quantity excreted by its waste, but also varies in close correspondence with the quantity taken in its food. It is therefore greater in carnivorous, and less in herbivorous, animals.

Hence the true or essential waste of the organism, in respect of this constituent, can only be determined from an analysis of the excretions of animals which have been kept for a day or two, either without food, or on a diet altogether devoid of nitrogen. In both cases the results are the same. The nitrogen of the egesta drops to a certain minimum; at which it remains for a considerable period.

The quantity of nitrogen evolved by the lungs and skin is at any rate so small, as scarcely to form an important element of calculation. And even the larger quantity excreted in the biliary resin, hardly deserves notice. It is in the uric acid, and above all in the urea, of the renal secretion, that this element is chiefly dismissed from the body as an effete compound. And hence it is from the urea found in such experiments that we may best deduce the probable rate of daily waste in the albuminous tissues; and the corresponding quantity of protein which therefore has to be supplied in the daily food.

From observations of this kind on the human subject, we may infer that, in Man, the albumen of the adult organism undergoes a loss of about 2 ounces daily;—a quantity which corresponds to scarcely more than $\frac{1}{1200}$th of the weight of the body. While if we suppose that a new-born infant, weighing six or seven pounds, consumes daily about ten or twelve ounces of milk, containing $3\frac{1}{2}$ per cent. of casein, the quantity of protein thus introduced into its alimentary canal would amount to the larger proportion of about $\frac{1}{270}$th of its total bodily mass.

The larger proportion of albumen thus consumed by the infant probably depends upon at least two causes. As a smaller* animal, it is subject to a more energetic waste of substance. And as a growing animal, it not only lays aside in its body a constant surplus of its income over its waste; but possibly undergoes a more active metamorphosis, that still further increases the proportion of its effete materials.

But, apart from the influence of age or size, there is no doubt that a careful comparison of the azotized ingesta and egesta would always show a marked disproportion between the two. There are indeed obvious reasons, why the nitrogenous constituent of any suitable food should always greatly exceed that quantity which is required by the strict exigencies of the organism. A part of the casein which is contained in the milk taken by the sucking-child, is often found to pass through the alimentary canal without being absorbed into the blood. And in the case of many other varieties of food, the insoluble state of the protein-compounds actually present affords a still greater obstacle to their absorption. In a proper mixed diet, however, we may detect some approximation between the presumable gain and loss. Thus the daily rations of the British soldier on home service include little more than 5 ounces of albuminous substance;—a quantity which is therefore little more than double the amount

* Ignorant as we are, both of the nature of this metamorphosis, and of the various stages through which it is conducted, there are reasons for conjecturing that the formation of the chondrin radicle generally precedes that of the substance which yields gelatin by boiling.

Supp.

* From researches by Frerichs, Lehmann, Bidder, Schmidt, Boussingault, Valentin, and others, we may estimate the daily waste of albuminous compounds, relatively to the whole body, in the undermentioned animals, as follows:—Rabbit, $\frac{1}{140}$th; Cat, $\frac{1}{170}$th; Dog, $\frac{1}{330}$th; Horse, $\frac{1}{700}$th.

of this material, which the waste of his body probably dismisses from his system within the same period of time.

2. The next group of alimentary substances is that of the fats, the composition of which has led to their receiving the generic name of *hydro-carbons*. They are found in both animal and vegetable food. In the milk, they are represented by its butter; the quantity of which amounts, on an average, to about $3\frac{1}{2}$ per cent.

The great variety of different alimentary substances of this kind is such as to preclude even their enumeration. The most important are stearin, elain, and margarin. The composition of these three fats may be generally stated as almost corresponding to single equivalents of carbon and hydrogen:— or, more exactly, to ten atoms of each of these elements, *minus* one of hydrogen, and *plus* one of oxygen ($C_{10}\ H_9\ O_1$; or $C_{79} + H_{11 \cdot 4} + O_{9 \cdot 6} = 100$).

The uses sustained by these constituents of the food in the organism are easy to indicate, but difficult to specify. The protection afforded by the fat of the body to its temperature, and to the mechanical safety of its internal structures, might perhaps be accomplished without involving any rapid waste and replacement of the material by which it is afforded. But the vast quantity of fatty matter which enters into the composition of the nervous system, and the primary importance of this delicate and energetic organ to the maintenance of life, entitle us to infer, that its functions imply such a rapid metamorphosis of its substance, as can only be sustained by the continual supply of new materials to replace those rendered effete. And the numerical phenomena of nutrition further show, that the process of respiration is constantly dismissing from the body an amount of carbonic acid, the proportion of which to the azotized egesta proves that it must have been derived more or less directly from an oxidation of the fatty, as well as of the albuminous, tissues. The quantity of fatty matter contained in the healthy organism strongly confirms these views; and thus helps to account for its dietetic importance. For, including all their varieties in the tissues just alluded to, we can hardly estimate the total hydro-carbons of the human body at less than $\frac{1}{4}$th or $\frac{1}{5}$th of its weight. And since they scarcely form $\frac{1}{600}$th part of the blood, it follows, that even assuming this nutrient fluid equal to $\frac{1}{6}$th of the corporeal weight, its fatty constituent amounts to little more than $\frac{1}{800}$th or $\frac{1}{900}$th of the fat which is deposited in the central and peripheric structures of the nervous system, and stored up in the adipose cells of other parts of the body. Such an estimate further entitles us to conjecture, not only that the quantity of fat taken up at any one time by the digestive organs is limited to a very small one; but also, that it either undergoes some important metamorphosis before reaching the general mass of the blood, or is very rapidly eliminated from this fluid.

3. The *hydrates of carbon* form a class of nutritional substances, the elementary composition of which is still more exactly indicated by their name. In other words, they consist of carbon, united with hydrogen and oxygen in those equivalent proportions of these two elements which are necessary for the formation of water ($C_{12}\ H_{12}\ O_{12}$). This group is a very large one: and includes, not only the various forms of cane, grape, and milk sugar, but a number of kindred substances;—such as dextrin, gum, cellulose, inosit, and, especially, starch. All of these organic principles, however various their physical properties, have nevertheless the same chemical composition. And many of them are easily converted into grape sugar; either by the excitement of a limited metamorphosis by an azotized ferment, or by exposure to the action of dilute acids.

The sugary ingredient of the milk forms about $5\frac{1}{2}$ per cent. of its quantity; and is the only representative of the hydrates of carbon which it contains.

The average amount of the substances belonging to this and the preceding group of alimentary constituents will of course vary greatly in the different kinds of food. Speaking generally, however, these two groups may be stated to predominate by turns in the food derived from the two kingdoms of nature. Thus while the hydrocarbons are chiefly derived from the fat of animal food; the hydrates of carbon belong even more exclusively to the starch and sugar of vegetable food. But, in strictness, no such marked difference can actually be made out between the two kinds of food in this respect. The milk, the liver, and even the blood of the animal, all contain sugar: while inosit, a substance closely allied to sugar, forms an important constituent of its various muscles. And not only do many plants contain large quantities of oily matter stored up in various parts of their tissues, but even the seeds of the cerealia, which form the best vegetable diet, present an amount of fat ranging from ·2 to 2 per cent.

The purposes fulfilled by these hydrates of carbon in the animal economy, offer a marked contrast to those subserved by the two previous groups. The protein compounds form what is eminently the basis of the organism; — the plasma from which are developed the blood and the tissues. They are thus *histogenetic* and *hæmagenetic*, as the phrase is. The fatty matters of the body not only form a large constituent of the active nervous substance, but are also retained and stored up in the more inert and passive form of adipose tissue. While the grape-sugar, into which the various hydrates of carbon are all finally converted, appears never to assume any permanent form in the body, but to be always rapidly eliminated from the blood. In what shape, or after what metamorphoses, it leaves this fluid, is at present uncertain. It is, however, probable, that like the hydrocarbons, these hydrates of carbon are essentially a species of fuel for that process of calorific combustion, which pervades the whole body, and which discharges its resulting carbonic acid by means of the respiratory function. And Liebig has adduced numerical data from the fattening of animals, which lead him to suppose, that these substances are also capable of undergoing a process of deoxidation, that converts them into fat, and thus enables them to augment the adipose tissue. But this view rests on very insufficient foundations*: and is curiously contrasted with that oxidation† of hydro-carbons into sugar, which the researches of various recent observers seem to indicate as one of the chief functions of the liver.‡

4. The importance of the *water* of the food is such as justly entitles this liquid to the rank of a fourth alimentary constituent. For it forms about four-fifths of the entire corporeal mass: and undergoes, at the various excretory surfaces of the skin, the lungs, and the kidneys, a continual expenditure; the replacement of which is obviously necessary to the maintenance of the proper composition of the body.

The way in which this large aqueous constituent facilitates the action of the various organs is not very difficult to conjecture. Their merely physical properties of hardness, flexibility, and the like, often seem chiefly determined by the quantity of the watery ingredient which they contain. And their far more recondite vital properties seem quite as immediately under its influence. Thus not only do its solvent powers appear to be eminently useful in furthering the minute division, and the local transfer, of various organic substances, but we are justified in conjecturing that it gives a more specific chemical assistance to many of those processes of metamorphosis which are so intimately connected with life. In both of these respects, it would seem to afford a special aid to the function of digestion. While that act of absorption, which conveys the dissolved contents of the alimentary canal into the surrounding veins, is greatly facilitated by the heightened diffusive energy which the low specific gravity of water enables it to impart to the fluids with which it has been mixed. And finally, the use of water in relation to the opposite extreme of nutrition—namely, to excretion—may be well exemplified by the urine, in which a highly poisonous product of life is continually washed out of the system, through the instrumentality of a stream of this universal solvent.

The details of death by thirst afford a fearful commentary on the above remarks;—although, from reasons which will presently be mentioned, it will be obvious that even these cases rarely afford us true examples of the strict exclusion of all entry of water from without the body. After a period of agonizing thirst, the most distressing symptoms of which seem to be referred to the dry and inflamed throat and fauces, the deficiency of water is gradually revealed by a diminution—which is almost a suppression—of the various secretions that normally contain a large proportion of this liquid: namely, the sweat, the urine, and the fæces. Increasing muscular debility accompanies this change; and is soon followed by delirium and coma, ending in death.

And, conversely, the benefits afforded by water seem to receive an almost paradoxical illustration from its effects in the opposite states of starvation and of fattening. Thus, as regards the latter process, animals are stated to fatten much more easily and quickly when allowed the free ingestion of this liquid. And Becquerel and Lehmann state, that when water is taken in excessive quantity, an increased amount of urea is excreted from the system of the healthy human subject.* While the researches of Bidder and Schmidt† show that, even after the withdrawal of all other ingesta, the copious use of water concedes to the starving animal a longer duration of life;—diminishing, not only the waste of its protein compounds, but those collateral results of the vital processes, which are exemplified by the excretion of urea, carbonic acid, and salts.

Hence water, which forms about 85 per cent. of the milk, is a universal constituent of the food of animals; and varies only in the proportion which its amount bears to that of the solid ingredients mixed with it, or dissolved in it. In some of the lowest forms of animal life, its relative amount is so great, that the remainder of the food is only present in the state of a very dilute solution. In certain aquatic creatures of this kind, the medium around the animal seems to form a dilute alimentary solution, which only requires an act of absorption by the outer surface of its body. And even in the higher animals, in whom the other alimentary constituents are

* The increase of fatty matter supposed to have been derived from these hydrates was calculated by subtracting the fat added in the vegetable food from the increase of the animal's weight; — this surplus being set down as due to augmented adipose tissue. Hence any error in estimating the fatty constituent of this food, on the one hand—or any neglect to calculate the watery and proteinous constituents of the increased adipose tissue, on the other—would partially account for the difference observed. And it seems not unlikely that both of these inaccuracies actually occurred in these observations.

† Assuming that such a metamorphosis really obtained, it would not be difficult to explain most of Liebig's results. For it is surely not impossible, that the presence of an excess of sugar in the liver might diminish the energy of this act; in other words, that an excess of the product might lessen the activity of the process. Thus the copious ingestion of sugar might check its formation, and diminish the metamorphosis of the fat supplied to the liver in the portal blood. And this retention of the fatty form might not only affect the hydrocarbons of the food, but also those which are possibly developed in the organism from its own proteinous constituents.

‡ Compare the remarks on the liver, at p. 401.

* An effect which is probably due to its favouring the absorption of a larger quantity of protein from the same amount of food.

† *Op. cit.* p. 314.

always taken into a stomach, or internal cavity, part of the total quantity of water which really accompanies them into the system is often introduced by the same mode of absorption. So that, although the amount of water consumed by the organism has probably a definite relation to the activity of the vital processes, the amount of this liquid habitually swallowed by any animal is greatly affected by the quantity introduced in other ways: namely, by the proportion contained in its solid food, the amount formed by the combustion of hydrogen in its body, and the quantity absorbed by its skin from the vaporous or liquid water of the surrounding media. Thus the apparently dry food of many herbivora is explained by the large amount of water, which is present as a chemical constituent of such food, and which accompanies its few digestible parts into the system. And the small amount of drink taken by many of the Batrachian reptiles is chiefly due to the active tegumentary ingestion last alluded to.

The quantity of water contained in the various kinds of food ordinarily made use of, will be referred to hereafter. But we may probably fix its average at about 75 to 80 per cent. (or about 5 lbs.) of the mixed fluid and solid food (about 6·5 lbs.) of the human subject.

5. The *salts* of the food constitute the fifth and last group of its constituents, and that of which we may be said to know less than any of the others. For, while many of the more important are easily recognized in the ashes of the various fluid and solid aliments in which they are usually introduced into the body, still we are often at a loss to know the precise state of combination in which they are originally present in the food, far more that in which they enter into combination with the organism itself.

In the case of many salts, we can, indeed, trace the actual changes of composition which occur in the organism. Thus the salts composed of the various organic acids united with the alkalies, are converted into carbonates, prior to their dismissal from the body in the urine. And it seems possible that even the sulphates are occasionally decomposed in the alimentary canal; their sulphuric acid being deoxidized into sulphuretted hydrogen. while their bases unite with the carbonic acid formed in the system.

Hence, although a careful and repeated analysis of the salts contained in the organism and in its total excretions, might afford some clue to the qualities and quantities of the salts which ought to be introduced in the food, it would not by any means represent the details of these demands. While it is hardly necessary to add, that no such series of examinations has ever yet been made; and that, however carefully conducted, it might easily overlook very small quantities of important ingredients. Many discrepancies, however, it would probably clear up; such as why animals which in one region seem indifferent to salt, in others seek it with the greatest avidity; — why the diet which produces scurvy in one person, leaves another little affected;—and finally, why the roving population of the South American Pampas can maintain a robust health on the fresh meat of the wild cattle which range these plains, while an apparently similar diet on the flesh of tame cattle has been known to destroy English soldiers.

The more essential salts of the food seem to be the chlorides and phosphates of the alkalies; and especially, the chloride of sodium, and the phosphate of soda. Lime and iron are also important bases. All of these ingredients are present in the salts of the milk; together with some free soda and potash, which are probably combined with its casein. The phosphates are in large quantity; especially the phosphate of lime — the predominance of which is doubtless connected with the exigencies of ossification in the fœtus.

Varieties of food. — The above grouping of the various constituents of the food, will afford us a valuable clue to the composition of its principal varieties. For however widely these varieties may differ from each other, they always contain representatives from each of the preceding classes. And the best food for any particular animal will always consist of such a proportion of all these constituents, as best corresponds to the demands made by the waste of its whole body, and to the peculiarities of its organs of digestion.

The food most natural to Man is a mixed diet. But though thus far omnivorous, he readily adopts an exclusively animal or vegetable food, according to the circumstances in which he is placed. And there are probably but few of the carnivorous and herbivorous animals, most properly so termed, in whom careful experiments would not detect a similar, though scarcely equal, capacity for such a change of diet. Thus the herbivorous Horse and Cow may be brought to eat fish and flesh; and the carnivorous sea-birds can be gradually habituated to the far more difficult change implied in their feeding on grain. But many of the frugivorous Quadrumana seem little susceptible of such alterations of diet. While there seem to be numerous Insects, which are not only strictly limited to a vegetable food, but even to certain species of plants, or particular parts of their structure.

The influence of any special variety of food on the human organism depends chiefly on its physical and chemical properties: — in other words, on its mechanical arrangement and admixture; and on the constituents which it presents; either originally, or as modified by the operations of cooking. Hence these are the chief points which will be noticed in the following short description.

It is obvious that the division of the various alimentary substances into solid and liquid, or food and drink, is an incorrect one. For, on the one hand, even the driest articles of solid food contain a large proportion of water of composition. And conversely, the purest liquids ordinarily made use of contain a certain quantity of solids, in the shape of dissolved salts, which are by no means indifferent to the organism.

In the following cursory view of the ordinary articles of diet, we shall begin by contrasting the general characters of animal and vegetable food. We shall then sketch the chief varieties of each generally made use of. And, finally, we shall attempt to estimate the proportions of each contained in a suitable dietary of ordinary mixed food.

It is to animal food that we must on the whole assign the first rank as an article of diet. For not only do the tissues of one animal necessarily contain most, if not all, of the organic and inorganic substances required for the construction of another, and in something like the proper proportions of their respective ingredients, but they are generally devoid of all noxious constituents. Besides these advantages, they offer the equally important ones of possessing such a structure, arrangement, and solubility, as materially aid their entry into the organism. Hence they are not only much more nutritious than an equal quantity of vegetable food, but are also digested and assimilated with far greater ease and rapidity. It is for this reason that the use of animal food is so much to be preferred in all circumstances where it is our object to avert the speedy exhaustion of the vital powers.

Against these advantages, possessed by animal food, we must, however, set off the disadvantages, that it not only contains some substances which (like gelatine and the horny tissues) appear to be either useless or even to require a speedy excretion; but that, as a rule, it is deficient in those non-azotized elements, which are so important to the maintenance of the combustion and heat of the organism. For the limited quantity of fatty matters which it generally includes rarely suffices to make these hydrocarbons a proper substitute for the copious amylaceous and saccharine constituents of vegetable food.

The main disadvantages of vegetable food are equally obvious. It generally contains but a small proportion of the protein compounds. And even this limited quantity is often virtually diminished by their insoluble state; or by the indigestible form which is implied by their mechanical arrangement in the vegetable tissues. Many of its amylaceous constituents are also rendered useless in the same way: being enclosed in insoluble envelopes, which effectually shield them from the digestive process; or having a composition which requires to be altered by a chemical metamorphosis before they can be fitted for absorption. These objections can be to a great extent obviated by the ingestion of a larger quantity of such food, as well as by a more protracted sojourn in the alimentary canal. But, besides these disadvantages, the inorganic constituents of certain kinds of vegetable food appear to be insufficient for the replacement of the loss consequent on the waste of the animal. Thus the ash of many esculent vegetables is peculiarly deficient in the important ingredients of soda and the chlorides. The poisonous materials contained in the tissues of some plants constitute another objection to vegetable diet; — an objection which is, however, generally obviated by the instinct of animals, and by the experience of Man, or by the purification which the process of cooking often affords.

Animal food. — The muscular substance, accompanied by more or less of its interstitial and investing fat and areolar tissue, forms what is called *meat* or *flesh*, in the ordinary acceptation of these words.

The mechanical subdivision of a mass of meat would of course afford us the microscopic elements of the above tissues; — namely, sarcolemma, sarcous substance, white and yellow fibrous elements, fat, and blood vessels; together with a certain quantity of blood, and of the nutritional fluids which saturate each of these textures. Its chemical composition varies, not only with the nature, but also with the age, food, habits, and individual peculiarities, of the animal yielding it. Hence it is impossible to give any definite account of its quantitative chemistry. We can only enumerate its principal constituents; and, in the case of some of the more important of them, approximatively estimate their amount. The protein-compound, that forms by far the greater part of the muscular fibres, is a substance which possesses characters closely allied to those of fibrin, and has received the name of syntonin. It is usually present in a proportion of about 15 or 16 per cent. The albumen of the juice which soaks the whole muscular mass, and the gelatin which is extracted from it by boiling, may each be estimated at about 2 per cent. Its extractive, exclusive of salts, amounts to about 3 per cent.; of which nearly half is dissolved by alcohol, half by water. This constituent has a very complex composition: osmazom, lactic acid, inosit, kreatin, kreatinin, and a variety of other substances, having been detected in it by the labours of modern chemists. The salts of meat form about $1\frac{1}{4}$ per cent. of its fresh substance, or about 5 per cent. of its dried mass; nearly three-fourths of their quantity being phosphates of the alkalies, and two-thirds of the remainder phosphates of the earths, with a little iron. The chlorides of the alkalies are about one-fourteenth of the entire ash. They are remarkably contrasted with the chlorides contained in the ash of the blood, by the great proportion which the chloride of potassium bears to that of sodium.

It is impossible to estimate the quantity of fat contained in meat as usually eaten. But even after the removal of all visible adipose tissue, Von Bibra has found fractions ranging from one-twentieth to one-fifth; the smaller amounts corresponding to the flesh of the Hare and Deer, while the larger (in the beef of Oxen) were perhaps partially due to a more or less artificial fattening.

The flesh of Birds contains less water and fat, and more albumen, syntonin, and kreatin, than that of most of the Mammalia hitherto examined. The muscular substance of Fishes contains a still greater quantity of albumen. That of the young of most animals is softer, and its fibres smaller and more digestible, than the flesh of the adult.

The artificial preparation of animal food for the table probably induces a variety of chemical changes. But the full import of these changes has yet to be made out. At present, we know little except some of the more obvious physical results which attend the processes of cooking. These are best seen in the cooking of meat.

The increased digestibility of meat which has been killed some time previously to being eaten, seems to depend, partly on the more uniform and softer consistence imparted by the diffusion of its juices, and partly on the imperfect decomposition which it has begun to undergo. The latter change to some extent prepares it for digestion, by rendering it more soluble. But any approach to absolute putrefaction reverses this advantage;—at any rate, in the case of Man, whose natural judgment would probably in most instances lead him to reject putrid meat, as alike disgusting to the senses, hurtful to digestion, and dangerous to health.

In the operation of roasting meat, the heat applied to the exterior of the mass soon converts its superficial portion into a dense, hard substance. This compact crust consists chiefly of albumen which has been coagulated by heat. It is of essential service, not only in moderating the heat afterwards applied through it to the deeper portions of the meat, but also in retaining its various liquid and volatile products, which would otherwise be soon dissipated in the gaseous or vaporous form. The moderate heat which permeates the mass probably aids the various juices of the meat in diffusing themselves throughout its whole texture; increasing its uniformity of consistence, and dissolving much of its gelatinous tissues. Its albumen is always more or less coagulated by the heat; though, where much blood is present, the colour and fluidity which it sometimes retains, appear to indicate an imperfect character of this change.* A variety of empyreumatic substances, which are developed chiefly in the more heated exterior of the mass, next add the savoury odour and deepened colour, so characteristic of this method of cooking. If the process be unduly protracted, it will obviously burn the harder outside shell, and render the coagulated and contracted mass within too dense, tough, and insoluble for easy digestion; while, if conducted too rapidly, the same combustion of the outside is of course attended with the loss of all the advantages of cooking in the raw central portion.

The changes induced by boiling meat, partially resemble those which are caused by roasting it. For both of these processes are probably accompanied by a coagulation of albumen, a solution of osmazom, and a formation of gelatine in the mass itself. But they differ greatly from each other in many respects. From the lower temperature applied in boiling, no empyreumatic substances are developed; while the water which conveys the heat to the mass always extracts from it a certain proportion of its soluble constituents. This extraction may be to some extent diminished by suddenly plunging the meat into boiling water, so as to coagulate the albumen of its outermost layers; and conversely, the extractive process may be favoured, not only by increasing the surface of contact, but also by delaying the coagulation of the albumen, and prolonging the period of the solvent action. Hence, where it is chiefly the broth or watery solution of the meat which is intended to be used as food, the mass is preferably cut in very small pieces, and the temperature of the water raised very slowly to a degree of heat short of ebullition, and maintained there for a long time.

The various modes of salting and smoking meat are chiefly intended to protect it from decomposition; hence they scarcely require much notice here. In the former process, however, the qualities of the meat appear seriously damaged*, quite apart from the mechanical disadvantages which both it and smoking often impart.

Fat.—In a purely animal diet, the amount of this oleaginous constituent is of indispensable importance. For, with the exception of that minute quantity of inosit or muscular sugar which is proper to the sarcous substance, the fatty matters contained in the various tissues of the body are the only representatives of the two groups of the hydro-carbons and hydrates of carbon, which this kind of food possesses. Hence the fat of such a diet has to replace, as it were, the starch of the vegetables which usually enter into a mixed diet; and thus constitutes the sole non-azotized or respiratory element of animal food.

And even in what are often miscalled vegetable diets, a large quantity of this animal substance is commonly added to the other ingredients of the food. At least there seems to be a strong impulse towards such an admixture in most of the vegetarian nations and races of modern times: — an impulse which is well exemplified in the butter or ghee so copiously added by the Hindoo to the rice that forms his staple food.

The quantity of fatty matter which may thus be taken into the system can scarcely have any definite limit assigned to it. In the Arctic climates it appears to attain a very

* This imperfect coagulation has been supposed to prove that the heat (154°) at which the blood coagulates, has not been attained. But the appearances in meat boiled at 212°, and the temperature of roast meat itself, render such a view very doubtful.

* The liability of persons fed on such meat to scurvy, can scarcely be exclusively referred to the privation of vegetables. For large numbers of people appear to subsist with impunity on fresh meat only (see p. 388.).

large proportion. And it is impossible to avoid connecting this maximum of fat in the food, with the large amount of heat that has to be evolved from the body in these cold regions, as well as with the energy of the combustion on which this evolution of temperature depends. As a rule, however, but a small quantity of fatty matter can be really digested at a time. Any excess over this amount is merely expelled from the intestinal canal with the fæces.

The digestibility of fat depends chiefly on two circumstances: — its mechanical arrangement, and its chemical composition. In the adipose tissue, the fatty substances are enclosed in large nucleated cells; the membranous walls of which consist of a proteinous substance that is rather difficult of solution, and yet requires to be dissolved before its contents can enter the lacteals as chyle. And the three substances (stearine, elain, and margarine), which form the greater part of the fat of the Mammalia ordinarily slaughtered for food, possess very different degrees of solubility. Hence they are by no means equally easy of digestion; the first resisting its influence much more obstinately than either of the other two.

An animal which is fed exclusively on fat increases in size during a short period. Its nutrition, however, soon suffers; and it finally dies, with those appearances of inanition which have already been mentioned as attending all attempts to maintain life by the ingestion of only one ingredient of the normal food. In the later stages of this process of starvation, its body gives off a repulsive odour, which appears to be due to the evolution of volatile fatty acids from the skin and lungs. The production of these acids may be regarded as probably due to an imperfect oxidation of the hydro-carbons accumulated in the organism.

The alimentary properties of various other tissues and organs of the animal body may be passed over with a very brief notice.

The *blood* itself appears to be a far less valuable article of food than its composition would lead us to suppose: — abounding, as it does, in the important protein-compounds of fibrin and albumen. Some authors have supposed, that its digestion is rendered difficult by the dense state of aggregation which its fibrin is so apt to assume in the act of coagulation. But however this may be, still its large albuminous constituent appears to be in a condition such as would eminently fit it for fulfilling the requirements of the organism. We are thus left to remark upon its almost total want of hydrocarbons *: as well as upon the contrast offered by its salts † to those of the muscular substance.

The *brain* and nervous centres are so rich in albumen and fat, as to form highly nutritious articles of food; especially when they are mixed with other substances, which are more capable of affording the requisite mechanical stimulus to the digestive organs.

The various *glands* possess a dietetic value which is derived, partly from their physical structure and arrangement, partly from their chemical composition. Thus, the dense mechanical texture of the *liver* and *kidney* must decidedly oppose their usefulness as food: while the bile and urine which they respectively contain, necessarily superadd the properties of these secretions to those of the proteinous parenchyma that forms the bulk of their mass. And conversely, from both mechanical and chemical reasons, the *pancreas* is highly digestible and nutritious.

The hard solid texture of *bone*, and its large gelatinous and calcareous constituents, together render it of comparatively little use as an article of food.

The *eggs* of oviparous animals contain, in addition to the embryo itself, a quantity of nutritive matter, which is destined for its nourishment during the process of incubation. Hence, the large eggs of many Birds form an excellent article of food, the dietetic virtues of which resemble, to some extent, those previously attributed to milk. The white of egg contains about 15 per cent. of albumen. The yolk is composed of about 20 per cent. of the same protein compound; together with about 30 per cent. of fatty matter—chiefly margarin and elain — in a state of subdivision and admixture which eminently adapt it to digestive purposes.

The general composition of the *milk* which forms the food of young Mammalia has already been mentioned. It only remains for us to notice its chief varieties, and the products which its artificial preparation adds to the bill of fare of the adult.

The peculiarities exhibited by the various kinds of milk, are chiefly referrible to the species of the parent animal, the date of its lactation, the nature of its food, and its habits. Thus the milk of the Human female* contains about half the quantity of casein, and two-thirds the butter, of that of the Cow: while that of the Ass, which is still poorer in each of these constituents, greatly surpasses them both in the amount of its saccharine ingredients (being as 3 to 2). The rich colostrum which is yielded in the puerperal state † soon gives place to a milk which is

* See p. 386. of this article.
† Compare pp. 332. and 389.

* From some analyses of this secretion in two persons, L'Heritier concludes that the milk of *Brunettes* contains nearly twice as much casein, as that of *Blondes*; together with about one-half more butter, and one-sixth more sugar. This statement confirms a belief generally entertained as to the superior qualifications of women of dark complexion as nurses. But, without much more extensive observations, it cannot be accepted as an established fact. If true, it would remarkably complete what we may venture to call the structural and functional homologies of the mammary gland, all of which concur in regarding it as a highly-developed offshoot of the general integuments.

† The composition of the colostrum seems to indicate, that it is partly derived from milk which has been concentrated in the breast subsequently to its secretion, by the re-absorption of a portion of

poorer in all the solid ingredients: and the further continuance of lactation appears chiefly to increase its casein and salts, and diminish its sugar. The copious ingestion of fatty or starchy substances seems to increase the buttery constituent. The over-feeding of a wet-nurse causes her to secrete a milk abnormally rich in butter and casein, and injurious to a delicate child. Finally, vigorous exercise appears to diminish both these constituents, especially the former.

Butter.— The composition of the butter contained in milk is as yet but imperfectly known. That of the Cow is stated by Bromeis * to consist of about 68 per cent. of margarine, with 30 of elain, and 2 of fatty matters specific to butter. The exact nature of the latter constituents probably varies in different animals, as well as in different specimens of the secretion; and also seems very liable to be altered by that rancidity which butter so easily acquires from a short exposure to the air. Such circumstances quickly give rise to the formation of a variety of volatile fatty acids:—which are known under the names of butyric, caprylic, capronic, capric, and vaccinic acids.

The dietetic value of butter can scarcely be rated too highly. It is probably by far the best and most natural form in which hydrocarbons can be supplied to the healthy organism. It is not only attractive to the taste, but is easily assimilated:—even by children or adults, whose delicate digestive organs resent the introduction of the ordinary adipose tissue of animal food. The quantity which may be advantageously consumed will of course vary with the nature and amount of other food, and with the rate at which combustion proceeds in the body. But the very large amount of this substance habitually consumed by the Hindoos, and by the dairy-men in many of the Alpine highlands of Europe—in the latter case often reaching a pound daily—is a striking testimony alike of its harmlessness to the digestive organs, and its value to the system generally.

Cheese.— The substance known by this name consists chiefly of casein; which has been precipitated from the milk in company with a variable quantity of its buttery constituent. Its dietetic value is of course very high. But its digestive properties vary greatly; according to the proportion of fatty matter and salts which it contains, the mechanical aggregation of its mass, and the degree of decomposition which it may have experienced.

Thus as regards its admixture of butter, we may distinguish three varieties of cheese:—one which is made from cream, or from milk with the addition of cream; one from pure milk; and one from milk which has been skimmed or deprived of its cream.

its watery ingredient. This view is corroborated by the fact, that colostrum-corpuscles have been found in the milky contents of the male breast.

* Annalen der Chem. und Pharm. Bd. xlii. s. 46. *et seq.*

In respect to its salts, the chief distinction hitherto established appears referrible to the way in which the casein has been precipitated from its solution in the milk. Where the process has been effected by the addition of rennet, the caseous deposit contains a large proportion—about 5 or 6 per cent.—of phosphate of lime. But where the precipitation has been produced by the lactic acid which is gradually developed in milk as the result of its own spontaneous decomposition, the deposit contains scarcely one per cent. of this salt. In such a case, however, the smaller amount of phosphates appears to be partially compensated by the presence of some free phosphoric acid.

The changes which cheese undergoes by keeping are chiefly manifested in the formation of various volatile fatty acids, that generally communicate their characteristic odour to the whole mass. Such alterations are usually most marked in those varieties of cheese, in which but a small proportion of rennet has been used, and much fatty matter is present. Hence they seem at least partially attributable to a metamorphosis—probably an oxidation—of the buttery constituents themselves. In addition to this change, however, the casein also undergoes a somewhat similar fermentation; which is accompanied by the production of oxides of casein, and volatile fatty acids. Occasionally the process is carried so far as to constitute a kind of putrefaction, in which the nitrogen originally present is given off in the form of ammonia. The highly poisonous properties which decayed cheese sometimes possesses, and the repulsive odour which it often gives off, may illustrate these statements.

The value of cheese as an article of food may be to some extent inferred from the large amount of its proteinous constituent, which often forms more than 70 per cent. of its whole weight. This quantity of casein would correspond to about 11¼ per cent. of nitrogen: a quantity far beyond that contained in any other ordinary variety of azotized food. But just as this unexampled chemical composition may suffice to indicate how largely such a proportion of the "histogenetic" principles would require to be diluted with the "respiratory" or "combustible" substances, in order to constitute a food in the true acceptation of the term,—so it partially explains the fact, that cheese is anything but easy of digestion. With many persons even milk is only digested with difficulty; so that much of its casein may be traced through the bowels, but little changed by the action of the gastric juice. And the mechanical aggregation of many kinds of cheese—their extreme hardness, dryness, and density,—often enable them almost to defy digestion. But minute division, cooking, or careful mastication, will obviate one of these objections; and the other is easily met by a proper admixture of vegetable food. With such precautions, cheese becomes a most valuable article of food. So that we need be little surprised to find the extreme value and importance assigned to this variety of azotized aliment amongst rural populations where meat is scarce and expensive. Indeed, the diet on which tradition states old Parr to have attained his remarkable age can hardly have been very unwholesome. And the natives of a country which, like ours, still boasts of large cheese-fairs in some of its country towns, can find little to wound their national pride in the quaint fancy of Mueller:— that cheese and freedom flourish together.

Vegetable food. — The general characters of vegetable food have already been alluded to. They are, however, modified by all circumstances which materially affect the arrangement or composition of the vegetable tissues. Thus young plants, or the younger shoots of plants, are much more easily digested than the harder and less soluble textures of the older organism. While the approach of fruits towards their maturity determines a series of physical and chemical alterations, which have the result of rendering them much more nutritious. The mode of culture, and the peculiarities of the soil, also exercise important influences on the resulting vegetable produce. Thus a rich soil, a warm climate, or a highly azotized manure, have all been noticed to increase the per-centage of protein contained in the corn grown under their influence. And the influence of such circumstances will, of course, be in some degree extended to the persons and animals, whose staple food is thus partially dependent upon them.

Corn.—The seeds of the *cerealia* are not only the most important of all the varieties of vegetable food, but may even be ranked above all other alimentary substances, animal as well as vegetable. The history of mankind sufficiently attests the truth of this estimate,— an estimate which is confirmed by the appellation of "the staff of life," that is applied to their chief product as prepared for food.

An inquiry into their composition explains this remarkable value, by showing that the nutriment which such seeds place at the disposal of the vegetable embryo they contain, has a close resemblance to milk, both in the number and proportion of the alimentary principles of which it is composed.

The *proteinous* constituent of all the cereal grains forms a considerable proportion of their total weight. In wheat it even reaches 22 per cent. of the dried mass. But in rye, barley, oats, and maize, this amount is diminished to about 15 per cent. And in rice and buckwheat, it may be estimated at not more than 7 per cent. In respect to the varieties of protein which are present, we find substances resembling all three of its chief modifications in the animal kingdom. Thus wheat contains a large quantity of vegetable gluten, and vegetable fibrin, which are respectively analogous to casein and fibrin; together with a small portion of vegetable albumen.

The *amylaceous* or starchy constituent, which represents the calorific elements of the food, also varies in quantity; but to a smaller degree than does the protein. It forms about two-thirds of the four first kinds of grain above mentioned. In maize and rice, however, it rises to about 78 and 86 per cent. respectively; apparently replacing the protein which is diminished here. This starch is associated with a variable quantity of sugar, part of which may probably be regarded as produced from its own metamorphosis. And gum is also present in small quantity.

The *hydrocarbons* are only represented by a small quantity of fatty and resinous matter; the greater part of which, together with the cellulose also present, passes through the alimentary canal without undergoing any digestion.

The *salts* found in the ash generally make up about 1 to 3 per cent. of the whole vegetable mass. As regards their bases, they are chiefly characterized by containing little lime in comparison with magnesia. The quantities of potash and soda experience great fluctuations: — which are probably connected with the natural or artificial peculiarities of the soil in which the corn has been grown. The quantity of iron is generally considerable. As regards the acids of these salts, the phosphoric greatly predominates; while the sulphuric is in but small quantity. And the chlorides, so important to digestion and nutrition, are almost absent.

The ordinary preparation of these different kinds of grain is such as to introduce some slight changes of composition. The grinding of corn into flour strips away the outer husk of the grain; and thus has the disadvantage of removing a part of it, which contains a much larger proportion of protein than its more starchy interior. The subsequent process of fermentation and baking converts part of the starch into sugar and alcohol, with the formation of carbonic acid gas. The slow extrication of this elastic fluid gives the bread a porous or spongy character; which has the advantage of greatly increasing the effective surface that is subsequently exposed to the action of the digestive fluids. Part of the gluten of the flour is also lost in the process. But the whole amount of both gluten and starch which disappears is not very considerable; probably not more than 5 per cent. This trifling loss, and the addition of about 30 per cent. of water, constitute almost the only noticeable differences between the composition of pure wheaten bread, and that of the flour from which it is made. Their effect is, to exchange the composition already mentioned in speaking of wheat, for about 16 per cent. of protein, and 35 to 40 of starch, in bread of a moderate dryness. But the advantages afforded by the spongy texture, and the intimate admixture of water, which are brought about in the process of making bread, are still further increased by a mechanical change produced in the starch-granules themselves. For, under the influence of the moisture to which they are exposed, most of these swell up and burst, and thus place their contents in a state much more accessible to the changes which are subsequently induced in them by the salivary and pancreatic secretions.

The various *leguminous* seeds contain a quantity of the protein-compounds which may be estimated as forming, on an average, nearly 30 per cent. of their weight; or half as much again as that present in the cerealia. The quantity of their starchy constituent is, however, much less; being barely 40 per cent. They contain a somewhat larger quantity of gum. They have also a larger ($3\frac{1}{2}$) per centage of saline ash; the several ingredients of which, though almost identical with those of the cerealia, approach each other much more nearly in quantity. From the few analyses hitherto made, it would appear that the quantity of alkaline bases is very large: but that potash predominates over soda; and lime nearly equals magnesia. And though the phosphoric is still the predominant acid, sulphuric and hydrochloric are also combined with the above bases: — the latter chiefly with soda.

The value of these vegetables as food will of course depend on the preparation to which they have been subjected before being eaten. When ripe and dried, their small proportion of water, and their great density, together with the little surface they expose, together render them almost impregnable to the attacks of the various digestive agents. And even after moderate mastication, their larger fragments pass with little change through the whole of the intestinal human canal.

But after careful boiling, which bursts their starch granules, dissolves their gum, and softens and breaks up their various tissues, they assume the proper digestive value to which their composition entitles them. So prepared for eating, their large constituent of vegetable casein renders them a most efficacious azotized food. While their considerable quantity of starch, as well as their comparatively uniform admixture of the particular salts most important to nutrition, gives them a completeness for dietetic purposes, which even wheat can scarcely be said to possess. Hence we are entitled to suppose that, if suitably prepared by cooking, some of these legumes might form a food sufficient for the maintenance of health.* At any rate, we may presume, that their dietetic usefulness is rather under than overrated; so that, on physiological grounds, their consumption as human food might be advantageously extended far beyond those limits which the custom of modern European nations (and especially of the English) seems to have assigned them.

The *potato*, the starchy tuber of a plant belonging to the poisonous genus of the *Solaneæ*, is an article of vegetable food, the properties of which render it a remarkable contrast to the preceding group. We may best sum up its average composition as consisting of about 75 per cent. of water, and 25 of solids. Of the latter portion, only one-tenth is composed of protein, which is present in the form of albumen and asparagin. Three-fifths of these solids are starch. The salts of its ash amount to about 1 per cent. They are chiefly characterized by the fact, that though they contain little lime, and scarcely any soda, they include a large amount of potash; which, in the fresh tuber, is probably combined with some of the organic acids present. The quantity of phosphates is also very small: — barely, one-fourth of that contained in the various cerealia.

The above sketch of the composition of this vegetable sufficiently entitles the physiologist to range himself with the economist in determined opposition to the predominant use of this vegetable as the principal article of food. We may dismiss from our notice all consideration of the social and moral degradation which, since its introduction with this object, have steadily followed such undue use of the potato as the staple aliment in various parts of Europe. We may even set aside those fearful outbreaks of pestilence in Ireland which, though produced by the quantitative failure of one crop, must surely have been in some degree fostered by a peculiar state of the constitution — itself probably founded, in part, on the qualitative deficiencies of the previous food. Our objections to the potato find a better excuse in such a composition as the above. Rough as is the above estimate, it nevertheless claims to be based upon analyses of unusual number and accuracy. It shows that the food to which it refers is wanting in some of the most important saline constituents of the body;—such as the phosphates, which are hourly leaving the organism in comparatively large quantity. And that, in addition to this grave fault, it contains so small a proportion of protein, that we may calculate about thirteen pounds of potatoes as the quantity which a man ought to take into his stomach, in order to replace the waste of his body by a sufficient quantity of the histogenetic constituent of the food. At least this would be the amount corresponding to the protein which long experience has shown to be enough, and not too much, for the daily ration of a soldier: that is, for the food of an adult male, in good health, and habituated to moderate, but not excessive, bodily labour. Lastly, we need hardly add, that the form and arrangement of the protein contained in the potato are such as would scarcely ever allow it to be as well digested as the protein contained in the bread and meat of the soldier's ration. Hence its less suitable quality would require to be compensated by a still further increase of quantity.*

But the mixture of potatoes with other alimentary substances, and especially with meat or milk, removes all these objections, and restores it to its proper rank in the scale

* Compare Daniel, chap. i. verse 12.

* A great increase in the capacity of the stomach is regarded by Dr. Todd as a not infrequent result of an almost exclusive potato diet, so common among the lower classes of the Irish.

of food. While its saline constituents, its potash, and its organic acids, admirably adapt it for that use as an anti-scorbutic which experience points out as one of its most valuable qualities.

Succulent vegetables. — The various succulent roots, fruits, and herbs made use of as articles of food, possess a composition which, though different in each particular instance, may still be comprehended in one general description. With little protein or starch, they include a variable quantity of sugar, pectin, gum, organic acids, and salts; united with what is always a large proportion of water.

Thus in the class of roots* represented by turnips, carrots, and beet-root, the quantity of albumen is not inconsiderable; — ranging from 1 to 3 per cent.†: and the pectin itself, (C_{12} H_{16} O_{10}) is in much more considerable quantity. The organic acids of these and the various fruits are too numerous to specify; but the malic, which is also found in the potato, is one of the most frequent. The fruits contain still less protein and starch than the above roots. The young shoots and leaves of the several varieties of cabbage include starch, and some albumen, as well as sugar. The fixed salts of these various esculent vegetables are little known. In fruits their quantity is small. But in the green vegetables it is larger. And, finally, in the pectinous roots, they form about 1½ per cent. of ash; in which Boussingault has found most of the ordinary acids and bases, with proportions somewhat approaching those seen in the potato; — save that lime and soda are increased, while phosphoric acid is diminished.

The nutritive value of these vegetable substances is therefore very considerable. Deficient as most of them are in the proteinous principle, they are of course unsuited for the maintenance of nutrition without the admixture of other azotized substances. The precise way in which their pectin is applied to the uses of the organism cannot at present be explained. But its composition is so far akin to that of the gum and sugar which accompany it, that we may conjecture it subserves purposes similar to those accomplished by these hydrates of carbon. The salts of such vegetables replace those lost by the body; and, although deficient in phosphates, seem to form what is, in most other respects, a tolerable compensation for the waste of excretion. Finally, their organic acids disappear in the blood, in which they probably undergo an oxidation that ultimately converts them into carbonic acid and water.

With respect to the two latter constituents, — namely, salts and acids — it is important for us to recollect, that there are many phenomena of health and disease which teach us, far better than our present knowledge of physiological chemistry, what is the true value to the organism of such compounds. The incontrollable longing of Man after variety of diet, appears to find vent chiefly in the cultivation and consumption of esculent vegetables of this class. While scurvy, and other dangerous diseases of the same kind, which are still too prevalent among us, may serve to advise us that, within certain limits, this instinctive taste represents a bodily want, the satisfying of which is not so much a concession to the cravings of luxury, as a payment of the just claims of health.

The *seasonings* generally added to food are rarely alimentary in the strict sense of this word.

Chloride of sodium, or common salt, is, however, a marked exception to this rule; being habitually taken by most nations, and eagerly sought after by many animals, both wild and domesticated. Its use in reference to digestion may be presumed to depend chiefly on its relation to the acid* of the gastric juice. But the alleged results of its complete withdrawal from the food of criminals, are such as to suggest an antiseptic action of this salt on the contents of the stomach, even independent of that exerted by the gastric juice itself. And the office it subserves with reference to nutrition generally, appears to be a still more obscure one. Its habitual ingestion seems to facilitate the process of fattening, as well as to increase the amount of excretion. The large constituent which it forms in the ash of the blood and of most of the tissues, probably has some reference to all these details.

The other seasonings chiefly made use of in civilized life may be divided into two classes; — acids, and acrid substances. The former consist of various organic acids; especially acetic acid or vinegar, and lemon juice. These seem to act mainly by stimulating the stomach; perhaps increasing the acidity, and with this the solvent energy, of the gastric juice. The various acrid substances — mustard, pepper, capsicum, garlic, &c. — are also supposed to stimulate the secretion of this fluid, by exciting a violent determination of blood to the mucous membrane of the stomach. Many of them are irritant poisons, when taken in undue quantity.

Stimulants.—Tea, coffee, and alcohol, are substances which, though taken with the food, are scarcely alimentary in any truer sense than some of the acrid seasonings just alluded to. Indeed, were the practice of chewing tobacco as prevalent as the use of these substances †, the leaf of this highly poisonous narcotic would be equally entitled to rank in the category of food. Still their

* Botanically, of course these parts are not "roots," though usually so termed.

† Frerichs, *Op. cit.*

* Compare pp. 332. and 349.

† An instance of the partial starvation of a large ship's crew on a long voyage was lately brought under the author's notice, in which the chewers of tobacco were alleged to have endured hunger far better than the other sufferers: whilst the smokers of this narcotic did not enjoy the same advantage.

habitual ingestion in company with other articles of diet, and the manner in which they modify nutrition, forbid them to be passed over unnoticed.

Tea and Coffee.— Tea and coffee present a marked similarity, not only in their composition, but also in that action on the nervous system which is their chief physiological effect on the organism. Both consist of an oil, with a certain quantity of tannin, united to an azotized vegetable alkaloid; which is called thein, or caffein, respectively, but possesses the same composition in both ($C_{46} H_{10} N_4 O_4$). As regards their effects on the system, both produce sleeplessness and cerebral excitement. But coffee stimulates the circulation much more strongly, and in some persons excites diarrhœa. While tea is more apt to produce muscular tremors and irregular cardiac action; and generally causes a constipation rather than a relaxation of the bowels. The dietetic use of the two is very similar. How far they promote digestion is doubtful. They seem, however, to lessen the drowsiness and cerebral inaction which often follow the ingestion of a large meal. Like alcohol, they probably* diminish the rate of waste of the tissues generally.

Alcohol in all its various forms—whether of beer, wine, liqueur, or spirits—is equally undeserving of the name of food. It is not a nutritious article of diet; but rather a drug, which has a specific stimulating action on the nervous system. As regards its ultimate destiny in the organism, it seems certain that a part of it leaves the body, unchanged, in the exhalations of the skin and lungs.

The fermented liquors enumerated above are generally taken with the food. And in many of them, the alcohol is associated with small quantities of sugar and other alimentary substances. Their several tastes and odours are due partly to these, partly to other admixtures:—such as the bitter of the hop in beer, œnanthic æther in wine, and the various products of distillation in ardent spirits. The per centage of alcohol in these different liquids may be estimated as being, on an average, 3 to 7 in beers; 7 to 20 in wines; and 20 to 50 in spirits.

Dietaries.— In ending this cursory view of the different alimentary substances, we may briefly inquire into the quantity and quality of the food which would be the result of their admixture with each other, in the proportions best suited to the maintenance of health.

From what has already been stated, it is obvious that, in constructing such an ideal diet, or in estimating the proper daily ration which ought to form the food of any individual or class of persons, it should be our first care to ascertain the presence of all the alimentary principles in suitable proportions.

* Since the above was written, the experiments of Boecker, Lehmann, and others, on which this statement may now be regarded as based, have been well discussed in an article in the Medico-Chirurgical Review for January, 1855.

At first sight, it might seem easy to calculate an efficient scale of diet, from no other data but those which the above law affords us. With these data, it might even appear that such a knowledge of arithmetic as is implied in knowing the rules of simple addition and subtraction would enable us to calculate an infinite number of dietaries. For, it would evidently be easy for us to take any forms of protein, hydrocarbon, or hydrate of carbon, and compare the known per-centage of their elementary substances with the similar elements of the carbonic acid and urea which represent the most important products of the waste of the body. Adapting the quantities of the former to those of the latter, we might thus arrange thousands of formulæ, in which food would always cover waste, and income exceed expenditure:—formulæ which, provided the human organism were really made up of similar figures, would, no doubt, give us equally definite and satisfactory results when carried out into practice.

A variety of circumstances, however, concur to invalidate such calculations, and reduce them to their true value:—viz. the results of a mere process of addition and subtraction, that only distort and obscure the facts on which they are founded. Such circumstances prove, that the end of these sums in simple arithmetic is no better than the beginning:—that they do but repeat, in a less specific, and therefore less truthful form, the various statements of the skilful chemist, on which they are all based; and that, if carried any further, they can only mislead the physiologist.

For instance, not all our existing knowledge of the composition of most of the substances commonly used as food, would enable us to construct a diet which would be certain to contain an exact proportion of all the necessary salts. For, in the first place, we must recollect the probable importance of some which are only present in very small quantity; as well as the value that similarly appears to attach to minute proportions of certain organic acids, and their compounds with bases. In the next place, we must remember that, both in animals and vegetables, these saline constituents seem liable to vary, in nature as well as amount, according to the peculiarities of the soil from which they are ultimately derived. It is not by any means easy to insure their presence. And a good scale of diet ought to provide against any danger of their deficiency, by adding so much of various fresh vegetables as would cover all possibilities of such an occurrence. Indeed, nothing short of such variety would make the saline quality of any food perfect.

A similar argument will apply to the quantities of all the other ingredients. The mechanical state of the protein and hydrate of carbon will have at least as much influence in determining their requisite amount as the quantity rendered necessary by the waste of the tissues. Hence, to this latter estimate we have always to add a large excess; such as will be sufficient to cover the surplus protein which passes,—

undigested or indigestible—from the alimentary canal. And the same caution may be applied, with still more force, to that substitution of hydro-carbon, or fat, for hydrate of carbon, or starch and sugar, which some authors have regarded as so easy and natural an exchange. In all probability these substances are not by any means convertible or inter-changeable in any scale of diet. The cell-wall of the adipose tissue is dissolved with great difficulty; its liberated contents are next absorbed in but small quantities; and they then pass through glands which apparently have a slow but definite office to execute upon them, before they are admitted into the general circulating current of the blood. And, lastly, the rudest numerical contrast of their final combustive metamorphosis with that of the hydrates of carbon, shows that they require the combination of a much larger quantity of oxygen * before they can leave the body in the form of carbonic acid and water.

The total amount of food required by the body is also exposed to circumstances which are just as certain to baffle all such calculations. For this important quantity will evidently vary with the rate of waste sustained by each individual :— and hence with the activity of his life ; the nature of his habitual exertion; and the state of his mind ; as well as with the climate, race, temperament, and education, which help to form the microcosm of every man's personality. The degree of variation which may be brought into play by each of these circumstances it is impossible to specify ; though it would often receive no inapt illustration from a comparison of the habits of the various members of a family or other smallest social aggregate.

Hence the true value of physiological chemistry, in respect to the principles of dietetics, is that of being an admirable guide to the general composition of a proper food. In this capacity, it is not too much to say that its *veto* ought to be absolute. But with this negative function terminates its practical usefulness. Our choice of the exact quantities and qualities of alimentary substances necessary to construct a perfect scale of diet, may indeed be sometimes explained by chemistry. But it must always be dictated by experience. And the dietaries of gaols, workhouses, and hospitals, corrected, as they have too often been, by the ghastly hand of Death himself, have fixed the limits of the food necessary for health, with an accuracy which, considering the price of human life that has been paid for it, ought surely to satisfy the most rigid economist.

From such sources of information we may deduce, that a healthy adult male, of active habits, requires daily about two pounds of solid food. Of this food, six or eight ounces are, preferably, meat. While, if the quality of such a diet be lowered (as, for example, by the introduction of much potatoes or rice), its quantity ought to be proportionally raised, so as to compensate this diminution of its nutritious characters.

Relations of digestion to nutrition generally.—We have thus specified the various alimentary substances which are normally submitted to the action of the digestive canal. And the functions of the different segments and structures of this tube have already, so far as possible, been assigned to each.

All these functions, however, together make up but a small part of the complex act of digestion. Nay, more, digestion itself is only a part of a still wider and more complex process of nutrition. And, further, the relation borne by digestion to nutrition is by no means limited to an absorption of new matter into the body ; but also involves a revolution or cycle of much of the existing substance of the organism, between those acts of ingestion and egestion, which mark the respective extremes of its nutritional life. Hence it seems necessary to end this description of the alimentary canal by a succinct enumeration of (1st) the series of phenomena which constitute the digestive act, and (2nd) the share which digestion itself takes in nutrition generally.

We may best review the various stages of digestion generally, by supposing that we could track a mass of mixed food through the whole extent of the alimentary canal, and could observe the changes which it gradually underwent in this course. Such a food must of course be assumed to consist of proper proportions of all the alimentary principles, in the states in which they are ordinarily found in any diet suitable for the maintenance of health in the human subject.

The entry of such a food into the mouth would mark the end of what is generally described by systematic writers as the first stage of digestion :— namely, the act of *prehension*.

The food having arrived in the cavity of the mouth, is next subjected to the operations of *mastication* and *insalivation*.

Of these two processes, the first effects the mechanical division of the food :— reducing it to small particles ; increasing, therefore, its relative surface; and hence preparing it for the action of all those secretions to which it is exposed in its further course through the alimentary canal. The mechanism of this act is greatly aided by the simultaneous admixture of the saliva. This liquid is added to the food in quantities that vary, according to its dryness and the consequent need of such an addition, from 4 (apples) to 80 (bread) per cent. of the alimentary substance that is undergoing mastication.

But *insalivation* also adds an important chemical influence to the preceding mechanical advantage. The united secretions of the parotid, sublingual, and submaxillary glands, and the mucous membrane of the mouth, together furnish a liquid mixture, which converts starch into grape sugar with the greatest rapidity and energy. The perfect

* It would not be difficult to point out, how these views concur to explain the preference of fat as a calorific food, by the inhabitants of cold climates.

and instantaneous character of this change, which is only paralleled by the similar efficacy of the pancreatic juice, quite distinguishes it from that slower and less perfect metamorphosis which other animal secretions and substances are able to produce. The absence of the high temperature, and the evident putrefaction, which are generally associated with the action of these latter, still further distinguish the specific metamorphosis due to these secretions. But the substance and secretion of any one of the salivary structures, seems insufficient for the production of this agent. The submaxillary glands, and the mucous membrane of the mouth can, however, together furnish it without any aid from the parotid.*

The mastication and insalivation of the food is immediately followed by its *deglutition*, which propels the pulpy or semifluid mass it now forms into the stomach.

On entering this organ, it is subjected to a special act of *gastric digestion.*

The energetic action of the mixed saliva is not affected by the gastric juice secreted by the stomach. Much of the starch of the food is probably converted into sugar during the short sojourn of the aliment in this cavity. The sugar thus produced would seem to be absorbed by the vessels of the gastric mucous membrane with extraordinary rapidity. The water, salts, and soluble organic compounds of the food are similarly taken up. And the gastric juice attacks and dissolves the protinous element of the food. The perfectness of this process of solution depends on the mechanical state of the substances concerned, and the quantity and efficiency of the active liquid. Of the resulting solution or peptone, part is immediately absorbed by the gastric vessels, while part passes on into the duodenum, in company with portions of protein, which have not yet yielded to the solvent process. Many of these portions ultimately become dissolved, and with the peptone that accompanies them, are taken up by the veins of the intestine.

The *intestinal digestion* of the food is a still more complex act. The chyme that enters the duodenum probably contains all the alimentary principles originally present in the food. But it includes them in very different proportions compared with their original quantities. And these proportions have very diverse destinies in connection with the digestive process.

The watery ingredient of the food, and the salts it introduces, probably have but to complete their absorption. The soluble calcareous compounds appear, however, to decompose the bile ; and to combine with and precipitate some of its acids in the shape of insoluble salts of lime.

* The experiment on which Bidder and Schmidt (*Op. cit.* p. 281) claim a similar efficacy for that of the mucous membrane of the small intestine, appears scarcely to warrant such a conclusion. Should its accuracy be hereafter established, it would be interesting to determine how far the glands of Brunn were concerned in the process.

The protein-compounds probably continue their course through the intestine, still undergoing (or rather completing) a gradual process of solution under the action of the gastric juice which accompanies them. Whether any special intestinal juice* aids this process, may at present be looked on as doubtful. And whether the quantity of bile usually added in the duodenum can really hinder it, in the way in which Bidder and Schmidt † have found that it suspends the power of the gastric juice out of the body, remains equally uncertain.

The starch of the chyme would seem to be converted into sugar, by the addition of a further quantity of an agent, similar to that which is furnished by the mixed secretions of the salivary glands and mouth. At any rate, the secretion of the pancreas, which is poured out into the duodenum with the bile, is gifted with the capacity of inducing this change just as rapidly as the mixed saliva itself.

The fatty constituents of the food are probably absorbed by two channels, if not by two processes. But the quantitative share taken by each of these, remains at present unknown. That a certain portion of the fat contained in the food is taken up by the vessels of the alimentary canal, seems evident from the remarkable difference in the amount of this substance, which is found in the organic residuum of the portal blood, and that of the ordinary systemic veins.‡ But the quantity thus absorbed can scarcely be large. It appears to consist chiefly of the more fluid elain. And hence there seem no valid grounds for the supposition of much assistance being given to its transudation from the digestive canal into the veins, by means of a saponification with their alkaline blood. A much greater quantity of the fatty matter of the food is taken up by the lacteals of the villi, and is conveyed from these vessels into the thoracic duct. The microscopic details of this process have already been mentioned. Hence, it only remains for us to notice its chemical relations to the various secretions poured into the small intestine, in the lacteals of which segment of the canal the white or fatty chyle is chiefly found.

The experiments and observations of Claude Bernard would ascribe the formation of chyle chiefly to the *pancreatic juice*. This secretion appears to have the power of separating fats into their acid and base. But the fact, that such a saponification is prevented by an admixture of gastric juice, or any other acid, would justify us in doubting whether the change really occurs in the acid chyme of the living body. And all the appearances of the chyle in the lacteals of the villi concur in representing their fatty contents as being not saponified, but merely in a state of minute division. The production of this condition, — which closely corresponds to that of

* Compare p. 349.

† *Loc. cit.*

‡ See Heller's Archiv. vol. iii. p. 487.; vol. iv. pp. 15—37. 97—132.

oily substances when reduced to an artificial emulsion,—would seem to be one of the chief offices of the pancreatic juice.

The evidence adduced by Bernard* in support of his views appears very conclusive. His experiments gave him the means of obtaining large quantities of pancreatic juice from Dogs. A mixture of this secretion and oil, when shaken together, immediately produced an emulsion of the most intimate kind, such as no other animal fluid which he examined could imitate. A similar emulsion within the body could be seen in the Rabbit, when fed on butter. In this animal, the pancreatic duct opens into the intestine comparatively low down. And hence there is, under such circumstances, a long extent of bowel above the orifice of this duct, quite devoid of white chyle; while below, the lacteals are distended with this fluid. And, finally, experiments on the healthy animal†, and observations on human disease, tend to establish the same conclusion. Complete artificial obstruction of the pancreatic duct, diversion of its contents from the intestine, and extensive disease of the secretory structure of the gland,—alike prevent the formation of white chyle.

The small quantity of the pancreatic secretion would, perhaps, indicate that much of the metamorphosis of starch is effected by the saliva. And, taken in conjunction with the neutral or feebly alkaline reaction of the bile, and the apparently small amount of alkaline intestinal juice, it may at any rate be regarded as throwing great doubt upon the old theory of a direct neutralization of the acid chyme in the intestinal cavity.

The precise share taken by the *bile* in the process of intestinal digestion, is even more obscure than that of the pancreatic fluid. It may probably be stated as follows:—

The bile is not essential to the solution or absorption of any one of the alimentary principles. Nor, on the other hand, does its presence check the conversion of protein into peptone‡, or of starch into sugar. But from the appearance of the fæces in jaundice and biliary fistulæ, it would seem that its admixture with the food limits and modifies the putrefaction of its animal constituent, and the acid fermentation of its vegetable portions; and thus far aids in its proper assimilation. While the constipation generally observed in such cases, indicates that the bile is also a stimulus to the muscular action of the bowels.

The absorption of fatty matter is, however, materially influenced by the bile. So that, when this secretion is altogether diverted from its accustomed channel, its absence from the intestinal canal reduces the quantity of fat taken up here to about one-fourth of that normally absorbed.

The quantity of biliary solids discharged with the fæces is but a very small fraction of that poured into the bowel;—probably not more than $\frac{1}{10}$th or $\frac{1}{15}$th. And much of this may be regarded as a precipitate; which is produced, partly by an oxidation of a small part of the biliary fats into resinous matter, and partly by the combination of the fatty acids of the bile with the lime taken in the food.

The details of the assistance given by the bile to digestion, are very obscure. But assuming the accuracy of M. Bernard's views with respect to the pancreatic function, we may conjecture, that it is the venous, rather than the lacteal absorption of fat, which is furthered by the hepatic secretion. This view agrees with the known capacity of the soda in the bile to unite with fatty acids in the form of a soap. And that separation of the neutral fats of the food into acid and base, which would probably precede such a saponification, is sufficiently explained by their sojourn in the intestine at the ordinary temperature; or by the direct effect of this kind which the pancreatic fluid could produce, supposing it not overpowered by the gastric juice. But Bidder and Schmidt offer the further suggestion, that even neutral fat is aided in penetrating the villus by the moistening of its surface with bile:—a view which they confirm from experiments with capillary tubes and dead animal membranes.

The continuous absorption of these various alimentary principles constitutes the chief share taken by the remainder of the intestinal canal in the function of digestion. And as this absorption requires contact, too rapid a transit of the canal, or too limited an extent of digestive tube to be traversed, present much the same appearances in the food, and produce a very similar effect on the organism. Thus the fæces expelled in intestinal fistula, on the one hand, or in diarrhœa on the other, alike exhibit a large quantity of undigested starch, protein, and fat; with unabsorbed bile and water. And the fatal exhaustion which often accompanies both of these states, is evidence of the virtual starvation which may thus be brought about.

From the little change undergone by proteinous substances artificially introduced into the large intestine, as well as from the comparative development of this part of the canal in the carnivorous and herbivorous classes, we

* In a mere enumeration of the chief digestive changes, all controversial discussion would be out of place. I shall therefore content myself with saying, that having seen this eminent physiologist perform the more essential of his admirable experiments abroad, and repeated some of them at home, I entertain little doubt of their substantial accuracy. And to the ordinary disparity between the value of the negative and positive results of experiment, one may add, that none of Bernard's German antagonists appear to have succeeded in procuring large quantities of the pure secretion. Indeed I think that a detailed criticism of these negative results themselves, would amply justify the retention (for the present) of Bernard's view.

† The inflammation which sometimes follows these experiments on animals, may hinder the absorption of fat in two ways:—either by attacking the substance of the pancreas, or by engaging the tissues of the villi themselves.

‡ Compare p. 349., on the action of the intestinal juice.

may conjecture that its absorptive powers are chiefly intended to be exercised on the water of its contents; and on the sugar and lactic acid produced by that slow metamorphosis, which dense starchy substances would here continue to undergo. But in animals like the Horse, whose aliment passes quickly through the stomach and small intestine into an enormous colon, it is difficult to avoid believing, that a more or less modified gastric juice accompanies the insoluble albuminous compounds of the food into this segment of the canal, and continues its solvent action during their long sojourn in its interior. It would otherwise be almost impossible to explain the nutrition of such animals. How far the large intestine can take up fat remains unknown. But it seems certain that its share in the absorption of this alimentary principle is very slight compared with that of the small intestine.

The entire process of digestion might therefore be described as consisting in the application to the food of a variety of agencies, such as mechanical division, solution, and metamorphosis. In whatever manner these are applied (either to the food as a whole, or to the several alimentary principles which form its constituents), and whether they operate in succession or combination—in any case, they all work towards the same object: namely, that of preparing the food for absorption by the vessels and lacteals which occupy the walls of the digestive canal. With this act of absorption, the function of digestion terminates.

The chief agents of this process of division and solution, we have found to consist of certain liquid secretions; which are poured into the canal, either by the ducts of several glands, or by the vast compound mucous membrane that lines the various parts of its cavity. In short, the food received into the intestinal tube, mingles with a large quantity of a mixed fluid; which itself represents the aggregate contributions of the salivary glands, the pancreas, the liver, the stomach, and the intestine.

But the more accurate researches which have recently been made on the nature and amount of these secretions, confirm a suspicion that has long been entertained with respect to some of them by physiologists. Comparing their quantity and quality with that of the fæces and the food, we can now confidently state, that but a very small fraction of their whole mass leaves the canal with the excrements; by far the greater part of it being reabsorbed into the vessels of the alimentary canal.

This proposition — so important to a correct appreciation of the true office of the intestinal canal, and of the relation of digestion to nutrition — has lately been placed in the clearest light by the admirable researches of Bidder and Schmidt upon animals. From their toilsome and accurate experiments, it would appear, that the total quantity of matter which thus leaves and returns to the circulation of an adult man, may be estimated at little less* than 20 pounds of liquid daily; of which about 3 per cent. consists of solids in solution. The importance of these "recrementitious" secretions to the system, is well shown by the results which follow the establishment of an artificial biliary fistula. Unless the ensuing loss of bile is compensated by the digestion of a much larger quantity of food, the animal so operated on soon dies of inanition. And it is probable that the exhaustion produced by diarrhæa, or by the discharge of the intestinal contents through an abnormal opening in the bowel, may be partially due to a similar loss of this and other rich organic fluids, which ought to be reabsorbed.

Whether the secretions experience any change prior to absorption — whether any of them are really modified, and thus far *digested* by their colleagues — remains at present in doubt. It may be conjectured, however, that they are so altered. At any rate, it would seem that, by provoking these secretions †, the whole system of a starving animal may be for a time invigorated and restored. But the chain of these phenomena is at present too indistinctly seen, and their connection with various other organic processes much too obscure, to justify us in doing more than offering this conjecture, as one of the most immediate explanations of certain well-known facts.

But we know enough to state that, within the limits of ingestion and egestion, lie two corresponding acts of absorption and secretion. Each of these is, so to speak, the coefficient of two elements. Absorption takes up food and secretions: secretion pours out, not only materials newly devoted to this purpose by the system, but others which have, in all probability, already subserved it many times before. The great mass of the intestinal secretions is thus continually revolving in a cycle:—forming a circulation the channel of which, placed in the intestinal canal, leaves and returns to the blood that flows in its walls; and only allows a very small offshoot of its current to reach the outer world, bearing with it certain of its effete particles.

The important chemical details of this circulation have yet to be won by sedulous and thoughtful "questionings of nature." But since, for the acquisition of such results, the liver offers what will probably be the easiest prize, it may be useful to point out how little even the vast progress of modern chemistry has hitherto been able to establish respecting its true physiological import. The portal blood,

* From the greater proportionate waste of small animals, it is possible that this estimate (22 lbs. for an adult weighing 140 lbs.) is rather too large.

† Some of the American Indians are alleged to eat clay with the object of allaying hunger. The drinking of water is well known to have a similar effect, and has been shown to increase the quantity of these secretions without causing a converse diminution of their density. And the benefit which a starving person derives from the minutest portion of food is sometimes so sudden and remarkable, that we can scarcely avoid referring it to the same explanation. (Compare 1 Sam. xiv. 27. 29.)

charged with the water, fat, albumen, salts, and extractive, which it has taken up from the food, and from the secretions of the digestive organs, reaches a large gland. There it breaks up, as it were, into two streams of fluid: bile, and hepatic-venous blood. And hence, the composition of these two fluid products, compared with its own, might be expected to give us a clue to the process by which they originate, if not to the action of the secreting structure itself.

Such an examination would show that the hepatic blood has lost almost all the fibrin, half the albumen, much of the water, and half the fat (even more of the elain) present in the portal vein. It has gained in extractive, and especially (ten to sixteen times as much) in sugar. And its pale corpuscles are increased in number.

On the other hand, the organic constituents of the bile are chiefly fatty substances, especially the fatty cholic acid and its congeners. The quantity and quality of most of these substances show that they have probably been formed in the liver: and hence that their presence in the bile is not to be explained as a mere transudation of certain dissolved constituents of the blood, followed by their concentration in the gland, such as might be alleged in the case of most of its salts.

But here for the present we rest. Sugar on the one hand, and certain fatty acids on the other, appear to be formed in the liver; at the expense of fat, albumen, and fibrin. Until accurate quantitative researches establish whether the disappearance of the protein-compounds is sufficiently accounted for by the total increase of extractive and of pale corpuscles in the bile and hepatic vein, the exact source of these substances must remain a mystery. Schmidt, indeed, suggests, that the fat of the portal blood is decomposed in the liver into the sugar and cholic acid which its elements would exactly make up. But while we are justified in giving every consideration to a view which seems so consonant with the facts hitherto known, we must be careful to remember that it is on these facts, and not on the neatness of any formula, that its value entirely depends. Unsupported by them, it would be a mere arrangement of certain letters and figures, devoid of all real significance, and destined to the oblivion to which thousands of its predecessors in the literature — not the science — of chemistry are daily being consigned.

Development. — The development of the alimentary canal, like that of other organs, offers a series of complicated changes, the details of which often have but little visible or direct relation with the future function of the part. Hence any minute description of the process would be quite out of place in this essay. The author therefore limits himself to a brief sketch of its general outline; and for all further details begs to refer the reader to the article "Ovum."

Just as the completely developed intestinal tube might almost be described as the involution of an extremely vascular cell-growth, so its origin distinctly refers it to those two germinal layers of the embryo from which such mucous and vascular structures are respectively derived. The centre of the early ovum consists of three layers; the upper or serous, the middle or vascular, and the under or mucous, lamina. A portion of each of the two latter is folded inwards, to form the rudiment of the alimentary canal. And the whole history of the subsequent development of this tube is little more than a recital of the various steps and processes, by which these mucous and vascular structures are so arranged as to result in the characteristic form, the numerous segments, and the complex structure, which have been briefly described in the foregoing pages.

The formation of the tube begins by the separation of the united vascular and mucous layers from the serous lamina immediately above them. An increase of this separation prolongs their attachment to the serous layer into a simple and rudimentary mesentery. Each end of the canal is then mapped out, by the conjoined laminæ being bent downwards and inwards, so as to give rise to two shallow pits or fossæ: which are named the *fovea cardiaca, seu aditus ad intestinum anterior*; and the *foveola caudalis, seu aditus ad intestinum posterior*. These two fossæ, however, do not correspond to the future mouth and anus; but to the cardiac aperture of the stomach, and to the middle segment of the rectum respectively. And between them, a lateral inflection of the conjoined mucous and vascular layers gives the canal two sides, the *laminæ intestinales*; which, like the similar vertebral plates of the serous layer, bound a shallow groove. This groove, the *fissura intestinalis*, is rapidly converted into a tube, by the closing in of its inferior or open surface. The process of closure begins at each extremity of the groove, and runs rapidly towards its centre; but is arrested here, so as to leave an opening or umbilicus, by means of which the intestine is connected with the umbilical vesicle that replaces the vitelline membrane and yolk. But there does not seem to be any direct continuity of the vitelline and intestinal cavities with each other through the channel formed by this umbilical ("omphalo-enteric") duct: — at least not such an aperture as to allow of the yolk itself being immediately received into the intestine. As the umbilical vesicle gradually removes from the intestine, this duct undergoes a corresponding elongation. Its canal becomes obliterated prior to the degeneration and disappearance of the tube itself.

The simple straight cylindrical canal, the development of which has thus been traced out, resembles the permanent intestinal tube of many of the lower animals; with the exception that, as above stated, it is deficient in both terminal segments. These it next acquires. And at the same time that it does so, it assumes the length, form, and convolutions, proper to the perfect intestinal tube.

As it already occupies the whole length of the abdominal cavity, any elongation of the canal will of course give it a curved shape. And since, at this period of fœtal life, the abdomen opens by a wide vertical fissure in the situation of the future umbilicus, the first bend of the intestine renders it convex forwards, and then protrudes it through this aperture. Here it adjoins the base of the umbilical duct; which opens into the point or angle of this convexity, so that the bowel appears like a bifurcation of the duct itself. The two forks of this bifurcation are soon produced into a spiral coil of intestine; which still lies outside the abdominal cavity, and only recedes into it at about the middle of the third month of uterine life.

At this stage of its evolution, the intestinal canal may be conveniently described as consisting of three portions: an anterior, which extends from the beginning of the tube to the umbilical coil; a middle, which is formed by this coil itself; and a posterior, which reaches from the latter segment to the end of the canal.

The anterior of these three portions may again be subdivided into three similar segments. The first, which gradually elongates from the blind end that was formerly the *fovea cardiaca*, is developed during the evolution of the thorax, so as to form the œsophagus. And it finally opens into the cavity of the mouth; which is itself developed from an involution of the skin, and from the united ends of the anterior visceral arch. The second or middle segment dilates, turns on its left side, and then bends transversely to the axis of the body, to form the stomach. The pyloric valve is only visible some time after this change has occurred. And the third or lowest portion of this anterior segment is converted into the duodenum.

The middle, umbilical, or extra-abdominal, part of the canal, is developed into the jejunum and ileum, the cœcum, the vermiform appendix, and part of the colon. In this process, the change of form undergone by the small intestine is limited to a mere increase in its length and in the degree of its convolution: — an alteration which is accompanied by a further elongation of its mesentery. The upper boundary of the large intestine is first seen as a constriction and change of calibre, which occupy a point some distance below the insertion of the umbilical duct. Such a situation of the future cœcum conclusively shows, that the vermiform appendix is not that permanent intestinal end of the duct, which Oken supposed it to be. This commencement of the large intestine next enlarges into a projecting pouch of uniform width. But the lower end of this pouch soon ceases to enlarge, and remains as the vermiform appendix. While its upper part, increasing in size, becomes the cœcum. The valve appears at about the tenth week. But the proper shape and size of the cœcum are only acquired towards the end of fœtal life.

The colon is developed from the lower part of the second, and the upper part of the third portion of the rudimentary intestine. The ascending colon is at first a simple straight tube, which, commencing in the pouch just alluded to, runs forwards along the spinal column, lying to the left of the numerous coils of the small intestine. The succeeding backward bend of this tube has at first a median position, which renders it parallel with (and close to) the ascending colon. But this part of the canal soon elongates; and, passing outwards towards the left side, forms the transverse and descending portions, as well as the sigmoid flexure, of the colon. Finally, the blind end which corresponds to the rectum is continually moved downwards by a gradual lengthening of the tube; so that it meets, and at last opens into, a cavity, which is sent inwards from the skin to form the future anus. The sacculation of the large intestine only occurs in the latter half of uterine life. The valvulæ conniventes appear still later, and are but rudimentary at birth.

The development of the various microscopic constituents of the canal may be almost as briefly summed up. The cell-growth (which is derived from the mucous lamina), and the fibrous tunic (which is developed from the vascular lamina), are at first very loosely united to each other. Hence they may be easily separated into distinct and comparatively plane strata; of which the fibrous has about double or treble the thickness of the epithelial one. The cells of the latter affect an elongated or columnar form at a very early date of fœtal life (about the sixth week). The various offshoots of tubes and other glands which are contained in the wall of the canal, are developed from a mass of cell-growth, which sprouts from the external surface of the mucous layer, and gradually acquires the definite form and cavitary arrangement specific to these minute structures. The larger accessory glands of the liver and pancreas are produced from a similar mass which lies external to the bowel: and they ultimately prolong their ducts so as to open into the cavity of the intestine.

The fibrous layer, which is at first smooth and homogeneous, soon becomes roughened into little projections, which ultimately take the shape of conical processes. These, as they enlarge, pass upwards into the mucous or epithelial layer. Some of these projections not only separate the various tubes and glands from each other, but, by a farther advance and enlargement, carry before them the general surface of the cell-growth. They thus form the future villi. While others — and by far the majority — affect a lateral, instead of a vertical, growth; uniting with their neighbours by cross ridges, which soon form a network, that extends between the tubes at all parts of their height, so as to constitute a matrix for these and the other structures derived from the mucous lamina.

Finally, the unstriped muscular fibres, and the white and yellow fibrous elements, repeat the ordinary steps seen in the development of these tissues generally.

Abnormal Anatomy.

Malformations.— The malformations of the digestive canal may be conveniently arranged in three groups:— 1. Those which appear to depend on an arrested or deficient development. 2. Those which are attended by an excess of size. 3. Those which can only be referred to errors of development, the causes of which are unknown; or to malformations of adjacent parts.

(1.) A deficient development of the whole tube may diminish either its calibre, its length, or both of these dimensions simultaneously. But malformations of this kind are rarely seen, in that marked degree in which alone they can be distinguished from from the differences which doubtless obtain in different individuals.

Among the results of a local failure of development, by far the most common is one, which we might expect to be so, both from the history of the evolution of the digestive canal, and from the analogy of malformations in other parts; namely, the absence of one or both of the terminal orifices of the tube, together with more or less of its adjacent segments.

Thus the imperforate anus, which is sometimes limited to the mere occlusion of the lower orifice of the bowel by a thin membrane, is, in other instances, associated with the absence of a variable extent of the rectum, and even of the colon, ileum, or jejunum. In such cases, a cord of more or less dense fibrous tissue generally replaces a variable extent of the absent segment of tube. The canal itself is usually dilated above its closed extremity. It may, however, communicate with the neighbouring urinary or genital cavities; or it may even open at the umbilicus.*

The analogous deficiency of the œsophagus is of less frequent occurrence than the preceding, and is but very rarely associated with it. Here the pharynx ends below in a blind extremity; generally forming a pouch, which sometimes communicates anteriorly with the adjacent trachea. The œsophagus below this pouch begins in a similar but narrower sac, which is separated from the pharynx, either by a membrane, or by a fibrous cord, or by an absolute interval of varying length.

The deficiency of the stomach occurs chiefly in acephalous monsters. It is sometimes accompanied by the absence of the duodenum, or part of the jejunum.

An incomplete evolution of the remainder of the tube is evinced, either by a local narrowness of variable* extent and situation, or by a closure and interruption which (*mutatis mutandis*) repeat the various grades of this malformation seen in the occluded œsophagus and anus. Or it may exhibit a somewhat analogous tendency of the more complex parts of the canal towards the simply tubular shape. Thus the stomach may be devoid, either of its cardiac sac, or of its pyloric valve; or may present a cylindrical form, precisely like that of the small intestine. Or the valve or pouch of the projecting cœcum, or its vermiform appendix, may similarly disappear.† The maximum of this imperfection renders the whole intestine a narrow cylindrical tube, in which it is impossible to distinguish between the large and small bowel.

Almost all the foregoing malformations, where excessive, are accompanied by other deformities, which affect the neighbouring organs. Thus the deficiency of part of the rectum is a common coincident of the monopodous state, in which the two lower limbs are fused into one.

(2.) The excess of development to which we may refer the second class of malformations of the digestive canal, consists in an increased length or width of the whole tube, or of any particular part of it. In the latter case, the large intestine, the cœcum, and the stomach are the segments most frequently affected. The other local malformations which we may ascribe to such an excess, are those of subdivision of the canal on the one hand, and the production of diverticula or supplementary tubes on the other.

Very few of the transverse subdivisions of the tube can, however, be regarded as really belonging to the category of excessive development. For even where these, as in the stomach, subdivide the cavity of the canal by imperfect septa, into abnormal portions, still the latter generally exhibit a diminished, rather than an increased size.‡

The longitudinal division of the tube presents us either with a septum, which separates its interior into two channels, that communicate again below; or with a double canal, of variable length and position.

The double cœcum which has sometimes been observed, might be regarded, either as a bifid or double state of the canal, or as the

* In that class of double monsters in which the trunks are distinct below, but united above in the upper part of the belly, a variable length of their two small intestines is sometimes similarly fused into a single tube, which bifurcates above and below. The seat of the lower bifurcation is sometimes occupied by a (probably true) diverticulum.

* In rare instances this narrowing is so great as to constitute a virtual occlusion. Thus cases are sometimes met with, in which the whole of the intestinal canal below the duodenum or jejunum constitutes a tube, which retains the formal separation into large and small intestine, but evinces its checked development by its narrow calibre, and by the dilatation or pouch above it, that terminates the normal segment.

† In some of these latter cases it is probable that the projecting cul-de-sac, which appears to be the cœcum only, is in reality the undivided rudiment of both it and the vermiform appendix.

‡ Some of these transverse subdivisions of the tube possibly imply a mere arrest of development in the site of the imperfect septum, without any excess of this process in the contiguous parts.

co-existence of a diverticulum with the normal pouch of this part.

The *diverticula* of the intestinal canal seem to be of two kinds, which differ, not only in the frequency of their occurrence, but also in their situation, form, structure, and (in all probability) in their nature or import.

The least common variety form pouches of variable length, width, and shape; which may spring from almost any part of the canal, but are usually connected with the small intestine. Their structure varies; but, as contrasted with the bowel itself, they usually exhibit more or less deficiency of the muscular coat.*

The *true diverticulum* differs materially from these. It usually forms a short tube of intestine, which leaves the ileum at from 1½ to 2 feet above its termination; by what is either a right angle, or is such as gives it an inclination towards the lower part of the bowel. Its width generally approaches that of the ileum, with which its cavity is continuous, by an aperture that is sometimes valvular. It possesses the ordinary muscular and mucous coats. The former exhibits its usual transverse and longitudinal layers. The latter also presents its ordinary structure: being occupied by villi, tubes, and follicles; and sometimes, by valvulæ conniventes of remarkable distinctness for this region of the bowel. Its length is generally about three or four inches. Its shape is more or less cylindrical, oftener contracting than expanding towards its termination. It commonly sustains vessels, and is attached by a kind of mesentery. Occasionally it exhibits, in addition to these vessels, a cellular cord that evidently contains the degenerated relics of some large artery. And finally, it sometimes extends upwards towards the umbilicus; and, in rare instances, opens here. From all these circumstances there can be little doubt of its true import being that assigned to it by Meckel; namely, that it is a highly developed and persistent portion of the duct of the umbilical vesicle.

(3.) The third or remaining group of malformations includes most of the congenital displacements of the digestive canal. These, as already mentioned, may be ascribed to two very different causes. The transposition or displacement of the tube within the abdomen, whether total or partial, is a fact for which the history of its development affords no explanation or probable secondary cause.† While the situation of any part of the canal externally to the cavity of the belly, is, in most instances, the mere result of a deficiency of the abdominal parietes.

The partial displacement of the canal generally affects the transverse colon, or some other segment of the large intestine; and, more rarely, the stomach. Its total transposition inverts the position of all the abdominal viscera with respect to the median line: so that, for example, the pylorus, the cœcum, and the ascending colon occupy the left side of the belly; while the cardia, the descending colon, and its sigmoid flexure, are found on the right, or opposite side.

The congenital inguinal herniæ form the most familiar illustration of the second (or extra-abdominal) class of displacements. And when a similar arrest of development involves the anterior wall of the belly generally, the abnormal situation of the canal may assume any grade, from that of a limited umbilical hernia, to an external situation of almost all the intestinal canal. While the deficiency of the diaphragm may allow a variable extent of the canal to occupy the cavity of the thorax. From obvious reasons, it is the commencement of the small intestine, which usually experiences this displacement. The stomach, above the hernia, is sometimes dilated.

Morbid Conditions. —*Size.* — Alterations in the size of the alimentary canal, though they chiefly affect its calibre, are generally associated with changes in its walls.

Constriction. — Narrowing or diminution of calibre is sometimes general, but is more frequently limited to a part of the tube. Its causes are various.

1. It often results from a process of contraction, which specially engages the muscular coat. Such contraction, generally passive, is well exemplified in the narrow empty tube, seen where the canal has for some time received no contents. Thus in persons who have died of starvation, the intestines are sometimes reduced to a tube, with pale thick walls, and a narrow calibre, like a tobacco-pipe. While a more local change of the same kind is often found in the empty segment of the intestine immediately below an obstruction, or an artificial anus. During its *rigor mortis*, the dead intestine often presents similar appearances. These may, however, be distinguished by their originating in a more active contraction, by their exhibiting a more marked, but less permanent character, and by their involving a less extent of bowel. And lastly, various irritants and astringents have been found to excite the muscular coat to contractions, which can more or less imitate the diminution of calibre producible by the preceding causes.

2. Narrowing may also result from the contraction of other intestinal tissues, besides the muscular coat. The constriction produced by the immediate or local action of the corrosive poisons on the alimentary canal, may be partially ascribed to their direct chemical influence on the various textures with which they come into contact. Such poisons, for

* Hence some anatomists regard these pouches as constituting a kind of hernia of the mucous membrane. But unless this view imply that they are, at least in part, of mechanical origin, it can only amount to a circuitous statement (and often an exaggerated one) of the above fact. It is however probable, that some of these diverticula really are the results of accident.

† In rare instances, the stomach or colon take a vertical position, which, to some extent, suggest an arrest of their development. But little stress can be laid upon such a conjecture, unless it be confirmed by other appearances of the same kind in these or neighbouring parts.

example, absorb the water of these tissues, coagulate their albumen, and thus corrugate and condense their mass. The narrowing which is produced by inflammation or by morbid growths, may be regarded as more mechanical. It results, either from the exsudation or deposit directly engaging more or less of the cavity of the tube; or what has a similar effect, from its ultimate contraction first reducing the size of the diseased part, and then trenching upon that of the neighbouring healthy parietes. Where the deposit of the new substance has been preceded by a loss of the normal tissue, — as often occurs in inflammation and ulceration — the constriction which is thus subsequently brought about is of course much more considerable.

3. To the above causes of constriction intrinsic to the tube, we may add several which are extrinsic to it. These are chiefly important, either by the inflammation they excite, or by the obstruction which constriction beyond a certain limit is apt to produce. Hence they will be hereafter alluded to, in connexion with those displacements of the tube, by which obstruction is most frequently brought about.

Dilatation.— An increase in the calibre of the digestive tube may be the result, either of distention of its cavity, or of relaxation of its walls, or of both of these causes conjointly. Thus that segment of the canal which is immediately above an obstruction, is always found in a state of distention: its dilatation being obviously produced by an onward transmission of the intestinal contents, to the point where their progress is arrested. And even in the absence of direct morbid obstruction, constant distention of the tube can to some extent imitate this state. Thus the colon of persons habitually constipated, frequently becomes enlarged to a vast extent. And the stomach of the rice-eating Hindoo, or the potato-eating Celt, often acquires a similar increase of capacity.

In many of these cases it is, however, probable, that the passive distention of the organ is assisted by an actual relaxation of its walls. In the enlarged bowels of obese individuals there can be little doubt that this is the case. And most of the diseases at present associated under the name of *ileus* exhibit, as one of their characteristic changes, a relaxation of the bowel, which may be distinguished from the preceding by its rapid occurrence, its morbid nature, and its usually considerable amount.

Thickness.—It is seldom, if ever, that the walls of the intestinal canal are altered in their thickness only. Apart from the obvious physical effects of distention and constriction, by which their tenuity is respectively increased and diminished, the coats of the bowel rarely undergo changes in this respect, without presenting some other appearances, such as betray a more important lesion. Indeed, the foregoing alterations in calibre are often associated with changes of texture.

Thus, in persons who have died from slow starvation, the intestines become extremely thin, soft, and transparent. A similar change sometimes accompanies that atrophy of the tube, which is produced by tubercular peritonitis or by diarrhœa, and is attended by an anæmic pallor of the canal. The dilatation caused by obesity is usually associated with an increased thickness of the intestinal parietes; a condition which has been compared to hypertrophy. Here, however, a careful examination will easily show that the real nutrition of the tube has by no means undergone an increase commensurate with that of its bulk. The bowel is indeed enlarged: but its muscular coat is softer, paler, and weaker; and its whole appearances are those of a thickening, which is chiefly due to an increased effusion of fluids interstitial to the normal solid structures.

Situation. — Changes in the *situation* of various parts of the canal are by no means uncommon. We have already alluded to the great freedom of movement which is natural to the small intestine *; and have specified the various regions of the abdomen which distention of the stomach † or large intestine ‡ may cause these segments respectively to occupy. We have also briefly mentioned the more frequent congenital displacements. We have therefore only to enumerate those displacements which are independent of the above causes.

The abnormal positions of the different parts of the intestinal canal are naturally divisible into the *extra-abdominal*, and the *intra-abdominal;* in other words, into those in which they are placed externally to the abdominal cavity; and those in which their change ra situation is within the belly, and thus allows them still to be bounded by its walls.

The first of these classes includes the various kinds of hernia: in which an unnatural deficiency or weakness of some part of the abdominal parietes allows a portion of the canal to be protruded through them; forming a displacement which, according to the situation of the protrusion through the wall of the belly, is called inguinal, femoral, abdominal, umbilical, or diaphragmatic hernia.

Amongst the second class of displacements, or those which are included within the parietes of the belly, we may first mention some, which are attended with few, if any, symptoms during life; and are, at least in many instances, a mere adaptation of the canal to external pressure.

Thus the habit of tight-lacing sometimes gives the stomach an hour-glass shape, sometimes thrusts down its projecting cardiac pouch, towards the left hypogastric region and the pelvis. In like manner, the bulk of the organ may be forced aside into various unusual situations by the pressure of any tumour in its neighbourhood. Thus, during the latter stages of pregnancy, the uterus so far encroaches upon the stomach, that the latter impedes the descent of the diaphragm, and

* See p. 340. † See p. 309. ‡ See p. 362. *et seq.*

thus claims a considerable part of the trunk which generally belongs to the thorax. The duodenum is so fixed as scarcely ever to be displaced, except when it is dragged out of its normal position, by displacements of the stomach or small intestine.

It is in the large intestine that such deviations of position are most frequently found. In the cœcum, however, they are by no means common; or if present, are generally limited to a descent of its dependent left extremity into the pelvis. The more frequent displacements of the ascending and descending colon seem usually produced by changes, which principally engage the segments that immediately succeed them. Thus the transverse colon sometimes appears to be wanting; being converted into a narrow arch, with the convexity upwards, and having sides which are no way distinguishable from the ascending and descending colon. The reverse of this state is even more common, in which the arch, instead of being horizontal, has its centre depressed towards the hypogastrium, so as to form an abrupt vertical bend, with the convexity downwards. Here the neighbouring ascending and descending segments of the bowel are, as it were, drawn into the increased length of transverse colon, so as to be themselves greatly shortened. And finally, the displacements of the sigmoid flexure, which are even more common than the preceding, resemble them in the modifications which they impress on the normal length and curvature of the tube. Sometimes they merely exaggerate the natural curve of this part; sometimes they lengthen it at the expense of the descending colon, or even of the rectum; and occasionally the curve is, as it were, transferred to the latter bowel. Lastly, the sigmoid flexure is sometimes preceded by a long segment of tube, which carries it over to the right iliac fossa; where it is so fixed, that the rectum which succeeds it, shares its displacement, is attached to the right sacro-iliac symphysis, and only gains the median line towards the middle of the sacrum.

The origin of many of these displacements is scarcely at present ascertained. But there is little doubt that they are often produced by tight-lacing, as above alluded to. Such a conjecture is confirmed by the fact, that they are almost limited to the female sex. They seem to occur most frequently in persons who have borne children.

We have next to notice a form of accidental displacement, in which the change of situation, though limited in amount, is much more serious in its results, leading to an obstruction that is usually fatal. It includes the various kinds of torsion, and the intus-susception or inversion of the canal.

In the *torsion* of the intestine, a portion of bowel is more or less twisted, either around its own axis, or around a centre formed by a variable extent of the neighbouring mesentery. The parietes of the tube are thus brought into contact with each other, with the effect of completely occluding its calibre. In what way this twisting is effected, or why it is not soon effaced by the subsequent distention of the bowel, it would be incompatible with the limits of this sketch to inquire.

In *intus-susception*, the obstruction is effected by the passage of a longer or shorter segment of the canal, with a portion of its adjoining mesentery, into the cavity of the next or following segment.

The anatomy of this displacement may be best traced by a brief narrative of the steps of its occurrence; at any one of which death may intervene.

Mobility of the tube is an essential condition of its production. Hence intus-susceptions are generally found in the small intestine, and sometimes in the large intestine; but rarely or never in the duodenum.

Irregular contraction of the muscular coat seems equally essential to their occurrence. Hence we often find them in dead bodies, as a result of the intestinal *rigor mortis*. While their occurrence during life can often be traced to a casual diarrhœa, which seems to form at least their exciting cause.

They are almost invariably produced by the reception of a superior into an inferior segment of bowel. It would therefore seem that they "originate as a kind of perverted peristalsis:—that, the longitudinal fibres remaining quiescent, the intestine is surprized by a transverse constriction, the rapid advance of which hurries the contracting portion into the flaccid and dilated part immediately anterior to itself."* The whole of this process appears to be well illustrated by the ordinary action of the œsophagus, the lower end of which tube undergoes a temporary intus-susception into the stomach at the end of every act of deglutition.†

The way in which the transverse contraction of a segment of intestine furthers intus-susception, receives some illustration by its frequent occurrence in cases where a polypiform tumour is attached by a pedicle or stalk to the interior of the intestine. Here the traction exercised by the stalk of the tumour on the wall of the bowel from which it takes its origin, appears to assist the muscular contraction of the segment which immediately propels the tumour itself, in producing the intus-susception.

The mechanical obstruction produced by an intus-susception is probably always an indirect result. It is perhaps aided by the obliquity of the received portion, the open end of which is always inclined towards the mesenteric border of the bowel. This obliquity seems due, partly to the pledget of mesentery, which shares the occupation of the outer or receiving segment of intestine; partly to the greater distention undergone by the free margin of the bowel above. In large intus-susceptions, the mesentery thus forms a thick strong cord, that not only ties down the bowel by its inner margin, but constitutes the

* Author, *Op. cit.*, p. 17.
† See p. 311.

axis of the spiral and dilated segment of tube around it. The congestion and strangulation of the vessels of the peritoneal fold, as well as of those of the invaginated bowel itself, soon cause a swelling, that fixes the innermost segment firmly in its abnormal position. An exsudation of serum and lymph next increases its size, at the same time that it renders these changes of situation permanent. The dilatation of the preceding part of the canal, by the fluids passed into it from above, often further exaggerates the above changes.

The sloughing which from all these causes finally ensues, sometimes has the effect of setting free the intus-suscepted segment in the cavity of the canal. Hence, if the patient survive until this separation occurs, the discharge of this segment from the bowels may terminate all the symptoms of obstruction; and leave the bowel at the site of the intussusception occupied by a ring of lymph, which gradually contracts into a firm cicatrix of fibrous tissue.

From the preceding changes in the size, shape, and situation of the digestive canal, we pass on to consider the abnormal conditions of its texture.

Softening is the first of these conditions which claims our notice.

In rare instances, this change engages the whole of the digestive canal, to which it imparts a semi-transparent gelatinous appearance, and a pulpy diffluent consistence. In this general softening, the walls of the canal are usually diminished, scarcely ever increased in thickness. Their colour is generally pale enough to warrant us in regarding them as in a state of anæmia. But they sometimes exhibit those various shades of discoloration which are present in the more localized forms of softening.

The latter are usually found in the stomach, where they especially occupy the cardiac pouch. But they are sometimes seen in the large intestine:—indeed, in most subjects, the mucous membrane of this part of the canal has a somewhat softer consistence than that of the small intestine.

It is in the stomach, in which the process of softening occurs with most frequency and intensity, that we may best notice the details of this change, and the degrees in which it generally engages the different tissues of the coats of the canal. Of these the mucous membrane is that which always seems to suffer first and most; in which the process appears to commence, and to which it is often limited. At first, the only noticeable change is a diminution of its consistence: a change which either occupies isolated patches of its surface*, or is spread over a considerable extent of the cardiac sac, rendering it liable to break down on the application of the slightest pressure. Hence if a portion be taken between the blades of the forceps, it will come away between them on exercising a very moderate traction. The mucous membrane next becomes absolutely broken down; so as to form a granular pulp. This pulp covers the subjacent tissues with a layer of variable depth; the deficiency of which, here and there, lays bare the submucous areolar tissue. The process may next engage this and the muscular textures; either imparting to the latter a paler, softer, and thinner appearance than natural; or implicating the whole thickness of the gastric parietes, and giving them a gelatinous appearance. A considerable thinning of these parietes almost always accompanies this change, and is sometimes so great as to cause the rupture of the organ, and the effusion of its contents. Finally, in extreme cases, the contiguous tissues of the belly, and especially the muscular substance of the diaphragm, become involved in an extension of this process from the stomach.

* These are sometimes the projecting summits of the ridges formed by its mucous folds.

The colour associated with this loss of consistence is very variable. In some cases, there is a complete anæmia of the gastric coats; in others, this term is rendered somewhat less applicable by the presence of one or two large veins distended with blood. In other instances, we find the softened part of the stomach coloured a variable shade of brown, red, or even black; according to the quantity of blood it presents, and the degree in which its hue has been altered by the gastric juice. Finally, in many cases the organ offers no appreciable contrast in this respect with its normal state.

It is probable that these softened states of the digestive canal are capable of being produced by very different causes. Even after setting aside all those instances in which the softening has been preceded by symptoms of inflammatory action during life; and all those in which it has been due to the ingestion of poisons which exert a direct chemical action of this kind; we may trace the process to three causes, which often coincide in its production, and the exact share of which it is therefore often difficult to estimate in any particular specimen. These causes are, putrefaction, digestion, and altered nutrition.

The amount of influence which has been exerted by putrefaction, might seem very easy to determine. But we cannot always estimate it by the date which has elapsed since death, or the temperature to which the body has been exposed; since its access and rapidity vary remarkably according to the state of the organism, and the nature of the fatal disease.

The capacity possessed by the secretion of the stomach for digesting its coats after death is one which will obviously depend on the nature and amount of this fluid present: and will, other things being equal, attain its maximum in the case of the sudden death of a healthy person, soon after the ingestion of food.

The softened state of intestines, which is often found in diarrhœa, fever, and other disorders, — as well as the peculiar softening*

* The characters of this softening appear to in-

of the stomach, long known to occur in ill-nourished infants, or in cases of hydrocephalus or brain disease, — point just as decidedly to the influence of an abnormal state of nutrition in favouring this state.

Lastly, there are many cases of acute disease, in which the softened stomach is more or less coloured by blood that has stagnated in its walls, where we have the additional difficulty of determining whether this congested condition preceded or followed death.

Hyperæmia.—The hyperæmia of the digestive canal constitutes an abnormal state, the correct appreciation of which is of great pathological importance. Of course, even the loosest interpretation of the term would limit it to an increase in the quantity of blood present in the vessels of the alimentary tube ; and would thus exclude a condition which is capable of being confounded with it : namely, a transudation of the mere colouring matter of the blood from neighbouring parts.

But there are many circumstances which render it very difficult exactly to determine the amount of true hyperæmia present in any segment of the digestive canal after death.

Thus, while there is little doubt that hyperæmia is a stage of almost all the processes ordinarily regarded as inflammatory, as well as of those which result in the deposit of adventitious growths, the examination of the digestive canal after death shows that this condition by no means accurately coincides with these processes. On the contrary, it is often absent in the very cases in which the symptoms during life might best entitle us to expect it. And conversely, it is often present where death has been the result of accident, or of disease no way referable to the organ which is the seat of the congestion. We are therefore bound to conclude : (1.) that the presence of hyperæmia in any part of the digestive canal does not necessarily prove this part to have been the seat of disease during life ; and, (2.) that the absence of hyperæmia in the dead structure does not disprove its previous presence in the living organ. And we have therefore to inquire : — (1.) What causes can produce it in the healthy tube? (2.) What circumstances can efface it from the diseased tube? And (3.), what are the marks by which we may recognize hyperæmia in the corpse, as a true and characteristic relic of diseased action during life?

It is to the phenomena of death, as this process usually affects the organs of circulation, that we must first look for an answer to the above questions. A very cursory allusion to these phenomena may suffice to indicate, in what manner they can by turns imitate, modify, or efface the state of true hyperæmia occurring during life. The *rigor mortis* of the dying arteries flushes and distends the capillaries beyond them with an abnormal quantity of blood. The degree, date and extent of this arterial contraction in different vessels, will obviously be capable of imparting almost any moderate amount of distention or congestion to the terminal networks they respectively supply. And at a later period after death, the gravitation of the now stagnant blood may distend the vessels of any dependent part of the body. But the congestion of one part implies—other things being equal—the drain of some others which are immediately contiguous to it. And hence the very occurrences which can cause moderate hyperæmia in a healthy segment of intestine, may at the same time produce a certain amount of anæmia in another ; and may therefore diminish — and, when moderate, remove — a state of simple congestion due to disease.

It would be easy to accumulate instances of the fact last alluded to. The state of really intense, though healthy, hyperæmia, which is present during the periodic activity of the stomach or other parts of the canal, rarely leaves any traces after death, unless in animals who are examined very speedily after this event, and before these new adjustments of its circulating fluids have had time to take place. In like manner, the increased vascularity of the intestines which accompanies cholera or diarrhœa is often just as completely effaced after death : — disappears, in short, in the same manner in which the redness of erysipelas and various other cutaneous disorders rapidly fades away in the first few moments that immediately follow the last breath.

But, even with all allowances for such sources of error, the condition of hyperæmia is one of the highest significance in the pathology of the digestive canal. It is, generally, an important sign of disease. And, with proper attention to its collateral circumstances, its import need rarely be misinterpreted. Thus, as regards the extent of the process, an intense and minute congestion is almost always morbid ; and is obviously much less likely to be removed by the phenomena of death, than one of more moderate hyperæmia. Again, a long duration of the abnormal vascularity, as in the hyperæmia of chronic disease, generally brings about such a definite and permanent enlargement of the vessels concerned, as evidently tends to enable them better to resist the action of these cadaveric changes. In other instances, a similar result appears to be produced by a process of exsudation around the vessels; and by changes in the structure of these tubes themselves. It must, however, be confessed, that we do sometimes meet with specimens of tolerably intense congestion of a part of the alimentary canal, where it is only from the presence or absence of corresponding symptoms during life, that we can conjecture whether the state of hyperæmia has preceded or followed death.

Of course, the mere hyperæmia of any network of capillaries may be determined in two ways : — either by an increased afflux, or by a diminished reflux, of the blood. But the

dicate that although it is probably preceded and assisted by an unhealthy state of the tissues of the stomach, the gastric juice is at least the chief immediate agent of the change.

first or "active" form of congestion may generally be distinguished from the latter or "passive" variety. The active hyperæmia is immediately attended by an enlargement in the calibre of the afferent arteries; the passive, by a diminution in that of the efferent veins. Again, the former usually has the colour of a tolerably scarlet or arterial blood; the latter, that of a darker and more venous fluid. Lastly, the active form affects chiefly the minute arterial branches and the capillaries; the passive is most prominent in the veins which come from these ultimate vessels. The hyperæmia of enteritis and of cirrhosis respectively, might well illustrate this contrast.

Amongst the varieties of hyperæmia, we may notice a more or less complete limitation of this state to the capillaries of particular tissues. Thus the microscope sometimes reveals a congestion of the gastric or intestinal mucous membrane, that specially engages those capillaries which surround the mouths of its tubes. In other instances, their blind extremities exhibit a similar state of injection. The exact cause of such partial hyperæmia is scarcely known. But the first of these varieties appears to be generally connected with a very limited amount of congestion. In accordance with this fact, it seems frequently to occur during or after death.

Hæmorrhage.—Hæmorrhage is by no means an unusual morbid occurrence in the digestive canal.

Of course, the mere presence of blood in some part of the alimentary tube, affords no proof that it has been derived from the vessels which occupy its walls. The blood which reaches the pharynx in cases of hæmoptysis, or of lesions of the nose, mouth, or pharynx, is often swallowed, and is thus introduced into the stomach or bowels. In like manner, blood effused into the ducts of the liver or pancreas, may be carried onwards through these tubes, so as to simulate hæmorrhage into the intestinal canal; or the blood extravasated into cysts, abscesses, and tumours, may find its way, through some abnormal opening, into the cavity of the bowels.

It was formerly supposed that, in many cases of hæmorrhage, the walls of the vessels remained uninjured; or, at least, unaffected by any definite solution of continuity: the blood being set free from its channels by "exhalation" through their porous walls. But we now know that this doctrine is incorrect; that the walls of even the finest capillaries have no pores of appreciable magnitude, such as are necessary for the transit of blood-corpuscles: and hence that the "extravasation" of these structures is, *ipso facto*, a proof that some blood-vessel has been ruptured. That, amongst the myriads of these minute tubes present, we often fail to detect the exact seat of the lesion, need, of course, little surprise us.

The frequency with which hæmorrhage occurs in the digestive canal, seems related chiefly to the number and delicacy of its vessels, to the nature of its tissues, and to the mode in which these structures are arranged with respect to each other. Amongst such predisposing causes we may especially notice, that the greater part of its large vascular supply breaks up into a vast and dense network of capillaries, which is placed in the closest proximity to the free surface of the mucous membrane. While the latter structure not only has a consistence which disease can readily reduce below what is necessary for the mechanical support of these delicate vessels; but is the constant seat of muscular movements, which agitate it in almost every conceivable plane.

The extravasated blood may either occupy the interstices of the intestinal tissues, or may make its way into the cavity of the canal.

The former case is much the less frequent of the two. As we might infer from the anatomy of the tube, the areolar tissue around the submucous stratum of vessels is by far the most frequent situation of such interstitial hæmorrhage.

The blood which is effused by hæmorrhage into the cavity of the tube itself may be either fluid or coagulated, arterial or venous, pure or mixed, changed or unchanged. With respect to the latter alternative, we may point out, that blood effused into the digestive canal not only becomes mingled with the various ingesta and secretions which may chance to be present, but gradually undergoes a kind of digestive process, that often has the effect of greatly modifying its colour and consistence. Hence, where the extravasated blood has been sufficiently exposed to this action, it will generally be found to have acquired a dark, grumous, or even black colour, and a peculiar tarry or almost pultaceous consistence. While conversely, if the effusion be excessive in quantity, or recent in occurrence, it may be pure enough to testify to its arterial or venous source. A small quantity of blood thus altered by digestion sometimes simulates the colour and appearance of inspissated bile. But by diluting the sanguineous mass with water, its dark-purple or blackish hue may be at once distinguished from the rich yellow colour which is proper to the biliary secretion. And a microscopic examination would, of course, assist (or even replace) this means of diagnosis.

The nature of these intestinal hæmorrhages is very various. Apart from mechanical injuries of the canal by foreign bodies applied to it from within or from without, we may classify (but scarcely separate) them into hæmorrhages from two sources: — from abnormal states of the vessels themselves; and from diseased conditions of the contiguous tissues.

As examples of the former variety, we may adduce the hæmorrhage produced by the rupture of an atheromatous artery; or the extravasation which occurs in cirrhosis from obstruction and distention of the portal veins.

The hæmorrhage of inflammation, of ulceration, of atony, may be referred to the second variety. But even here, just as it is evident that lesions of the vessel themselves always constitute the immediate cause of the extravasation, so we can hardly doubt that such lesions may (and often do) form a predominant, though not an exclusive, element in the process.

Inflammation. — Inflammation constitutes the most frequent and important of all the morbid conditions of the alimentary canal. Indeed, there are very few of these conditions with which it is not more or less directly concerned. It is generally, if not always, preceded by hyperæmia; often by downright hæmorrhage; and itself usually precedes the occurrence of ulceration and gangrene. It is the necessary result of mechanical injury to the various tissues of the tube; and is often an immediate consequence of the diseases or injuries of neighbouring organs. There is little doubt that it is often concerned in the production of those conditions which we at present include under the name of hypertrophy. And it is also capable of being evoked by the presence of adventitious growths, even though their origin may be regarded as independent of its presence. Finally, it constitutes one of the most characteristic phenomena by which various diseased states of the blood declare their influence on the system.

Such a diversity in the forms of the inflammatory process, as it affects the intestinal tube, might well lead us to expect variations at least as considerable and numerous in its nature. These, however, the space allotted to the present article will not allow us even to sketch. As little can we enter upon the difficult subject of its true pathological relations to the other morbid processes just alluded to. We must be content to accept the term inflammation as it is ordinarily made use of; and to enumerate its appearances, as they are usually seen in the dead body.

The mere existence of congestion we have already found to be no certain indication of the inflammatory state; but, on the contrary, one which would often deceive us, if viewed in this light. And though the presence of an exsudation forms a test which is far less frequently fallacious, yet even it requires some qualification, before it can be accepted as tantamount to proof of inflammation. For just as, to speak physiologically, it is the very office of the blood-vessels to mediate and permit an exsudative process of definite nature and amount, so slight differences of the exsuded fluid in both these respects, from that normally poured out, are not even incompatible with health, much less characteristic of inflammation. Hence, in saying that "exsudation" is a main feature of inflammation, we are using the word, not so much to express an isolated fact, as to imply a comparison: — an exsudation, of such a quality, and in such a quantity, as to offer a marked contrast with the specific fluid which is poured out by a secreting organ, on the one hand; or with the healthy nutritional fluid which bathes the interstices of its tissues, on the other. Of the two contrasts thus implied, that of quality is obviously much the more important. Thus, while the copious interstitial juices of the swollen but flaccid intestine of a very corpulent person, offer little difference from those of the typical healthy adult, save in their (so to speak) more diluted state, — or while the intestine of a dropsical abdomen is chiefly enlarged by an increase of the ordinary fluid of its submucous tissue, — the vessels of the inflamed alimentary tube take on what is more or less a new, as well as an increased action; by virtue of which they pour out, into the tissues or the cavity of the canal, fluids which are very different to those normally present in this situation. Using the term "exsudation" in this restricted sense, we should scarcely do wrong in regarding it as the chief feature of the inflammatory process; and as an appearance which, when seen accompanied by the ordinary marks of hyperæmia, quite entitles us to affirm that the part in which it is situated, was the seat of inflammation during life.

And not only does the presence of exsudation form the characteristic mark of inflammation, but the basis of the classification under which we may best arrange the varieties of this process.

Thus according as the characters of mucus, pus, or amorphous protein, predominate in the exsudation poured out, we distinguish the process which has given rise to it as *catarrhal*, *puriform*, or *croupy* inflammation. The rapidity of its effusion is at least a frequent and important element of these peculiarities which are summed up in the epithets "*acute*" and "*chronic*." And finally, as regards its extent and situation, it not only ranges from an inflammation of the mucous surface only, to one which successively involves the subjacent muscular and peritoneal coats, but may even specially affect the submucous areolar tissue of the canal, or engage certain parts of its secretory apparatus in the shape of its tubes or follicles. Each of these modifications will be noticed in a few words.

The *catarrhal* inflammation of the mucous membrane offers precisely the appearances seen in catarrh of other mucous surfaces. The numerous vessels of the membrane exhibit a state of more or less intense hyperæmia, giving it a corresponding shade of that red colour which is generally producible by vascular injection. This increase of vascularity is stated by Rokitansky to be chiefly visible, sometimes in the villi, sometimes around the follicles. But it seems to me that its being limited to the latter is often due to the contraction of the villi * having thrown back the blood they contain, into the adjoining follicular network with which they anastomose. The exsudation thrown out in this form of inflammation, may be traced in two situations: — in the textures of the canal itself, and in

* Compare p. 54.

its contents. In the former, it gives a softened, swollen, relaxed, and watery appearance to all the coats of the tube, and especially to its epithelium and submucous areolar tissue. In the latter, we notice certain changes in the fluids poured out upon the inner surface of the tube. The contrast between these fluids and those which are present in health is probably closely analogous to that which obtains in other catarrhs. The specific normal secretion is arrested, and is replaced by a variable (usually a large) quantity of a thin watery fluid. The effusion of this fluid coincides with the detachment of the proper epithelium of the mucous coat from the subjacent basement membrane ; a process that is generally followed by the shedding of large numbers of imperfect or abortive cells, which take their origin in the same situation. The admixture of this cell-growth imparts to the catarrhal exsudation its well-known gelatinous or mucous characters, and viscid consistence; properties which the microscope shows are partially due to the solution and rupture of these delicate cells, causing the escape of their contents into the surrounding fluid. The latter is either transparent, or of a cloudy, whitish, reddish, or grayish colour. The last of these appearances, when not due to an admixture of foreign ingredients, is mainly derived from the quantity of these cells, many of which generally assume more or less of the characters of pus. The reddish hue is due to an admixture of blood, by that process of hæmorrhage which so frequently results from congestion in the delicate mucous membranes.

The *puriform* variety of inflammation might, at first sight, seem scarcely worthy of distinction from the catarrhal. For the two merge into each other by innumerable gradations in the character of their exsudation. And the general tendency of catarrh of the mucous surfaces, to end in the production of pus, is too well known to require any comment. But while there always seems sufficient reason for distinguishing it as a separate stage of the inflammatory process in the digestive canal, there are circumstances which render it not improbable that the mucous and puriform inflammations of the intestinal canal are often distinct, both in their origin and nature. Thus there are some catarrhal affections of the bowels, in which lapse of time seems to have no effect whatever in exchanging mucus for pus ; while there are others in which this morbid product appears to be formed very speedily, or even at once. And that there are many cases which we should find it difficult to assign to one or other of these divisions, is an objection which would equally apply, not only to all the other varieties just alluded to, but to almost all the classifications we are compelled to use in describing the various results of disease on the healthy organism.

The presence of pus in any considerable quantity, is of course easily recognized by the glairy consistence and yellow colour it imparts to the exsuded fluid, as well as by its microscopical characters. It is usually accompanied by a swollen and sodden state of the various textures, such as greatly exceeds that noticed in the catarrhal inflammation. The redness and vascularity of these tissues is sometimes also increased in intensity. Often, however, the bowel acquires a grayish or ashy gray hue; or a dark reddish brown, or even slate-colour. The latter appearances are chiefly characteristic (as Rokitansky points out) of the duration of the disorder. It may be conjectured that these varieties of colour depend upon phenomena of at least three kinds. The paler tint, where not due to an interstitial deposit of pus, seems dependent on an abnormal influence which the disease exercises upon the circulation of the part, obstructing in some way the flow of blood in its vessels; an obstruction which the microscope permits one to suspect is rarely due to the mere physical effects of the surrounding exsudation. The various shades of red and brown appear to be determined by the changes undergone by blood, which has either stagnated within the vessels or — what is much more frequent — been extravasated from them. And the darker bluish or blackish tints are evidently caused by a variable quantity of black pigment, which probably forms the last relics of a similar degeneration of the blood, in the shape of masses of accrete (and now insoluble) colouring matter. With ordinary care, an admixture of biliary colouring matter can rarely be mistaken for these abnormal products. The production of pus may, however, take place in a less diffuse form, and by a much more rapid process, than that which causes the discharge of puriform mucus from an inflamed intestinal surface. These acute local suppurations, as we may call them, often at once strip off the whole of the cell-growth that normally covers the basement membrane of the mucous coat ; and then immediately proceed to erode and ulcerate the subjacent textures. These ulcerations seem peculiarly liable to form sinuses, by extending in various directions through the loose and yielding submucous areolar tissue. In rare instances, scattered abscesses are found in this situation ;—abscesses which are occasionally so isolated from each other, as to appear due to a process of purulent infection by means of the vessels themselves, and not to any mere extension of a continuous suppurating cavity. Finally, in extreme cases, the whole of the tunics become so infiltrated with pus throughout, as to form a soft or pulpy yellowish-gray mass ; which breaks or tears up on applying the slightest violence ; and, if life be sufficiently prolonged, becomes converted into a rotten membranous slough.

The *croupy* or *diphtheritic* variety of inflammation is distinguished, as its name implies, chiefly by the greater consistence of its exsudation ; which, in well marked cases, forms a more or less solid, opaque, white, or yellow mass, and is generally moulded to the shape of the inflamed surface, as a false membrane of variable thickness. It is almost always the result of a rapid or acute inflammatory process. Hence it is for the most part found connected with an intense redness and vascularity of the whole depth of the mucous membrane. And this appearance, which often extends to all the other tunics of the bowel, in some instances rapidly merges into a sloughy or even gangrenous state.

The exsudation of this croupy lymph occurs in a variety of morbid conditions. As an idiopathic disease of the canal, its effusion is very rare. In some of the exanthemata, and especially in scarlet fever, it is occasionally poured out over a very large extent of the inflamed mucous surface of the alimentary tube. In the tuberculous cachexia it is also now and then effused. In the inflammation produced by mechanical injuries, we may generally observe it; mingled, of course, with blood, where there has been any lesion of the blood-vessels. Finally, in cases of poisoning by irritant substances, its presence is by no means uncommon. Here, however, it is important to distinguish it from the false membrane which is often produced by the chemical effect of the poison on the membrane itself, and on the exsudation it subsequently pours out.

The morphology of the proteinous mass poured out under these very different morbid states, seems to be even more variable than its physical and chemical properties. The observations which the author has hitherto been able to make, would lead him to infer the following conclusions: —(1.) The croupy exsudation of the intestinal mucous membrane generally contains a considerable proportion of a cell-growth; which is an abortive epithelium, homologous with that of the healthy structure. (2.) The amount of this constituent attains its maximum in the tough white lymph thrown out during the acute inflammation of a previously healthy organism; for example, in the lymph of the inflammation that follows mechanical injuries of the bowel, or in the croupy casts of the intestine, sometimes voided in the earlier stages of scarlet fever or cholera. (3.) The form of this constituent is never that of the columnar cell proper to the healthy membrane; but, even when best developed, rarely exhibits more than its cytoblast, devoid of an outer cell-wall. (4.) The degeneration of these cytoblasts, as marked by the disappearance of their distinct nucleus, and the appearance of more refractile and granular contents, mark their transition to the characters of true pus-corpuscles; which thus become admixed with the croupy substance, and communicate to it the softer consistence and yellower colour of pus. (5.) The minimum of this modified cell-growth is found in the chronic forms of inflammations of the mucous membrane, and in the cachetic states of the system;—for example, in the exsudation associated with the tuberculous state. (6.) The bulk of such deposits is a mass, which generally has a yellowish colour, and is rarely mixed with small masses of black pigment. This mass possesses a soft friable consistence, and presents an amorphous granular appearance under the microscope. In exceptional cases, it varies from this description :— in the firmer deposits, by offering an indistinctly fibrillated texture; in the softer, by exhibiting numerous highly refractile (and probably fatty) molecules of variable size. (7.) The application of re-agents under the microscope, seems to indicate a corresponding variety of composition in these various forms of the croupy exsudation. At any rate, this very imperfect mode of examination permits us to conjecture that these exsudations consist in great part of protein-compounds, which possess very different degrees of solubility in different cases, and are capable of undergoing a partial degeneration into a fatty material.

The *acute* and *chronic* varieties of inflammation, like the preceding, merge into each other by infinite shades of resemblance. But they are contrasted by a number of circumstances, all of which seem more or less dependent on the rate and duration of the process.

Thus the *acute* inflammation presents a maximum both of hyperæmia and effusion; the latter having usually either a croupy appearance, or a more or less purulent composition. It involves a greater depth of the mucous membrane ; and often spreads to the subjacent muscular and peritoneal coats, so as to cover various portions of the latter with lymph. In its most intense form, it may even convert the whole of the intestinal parietes into a comparatively uniform mass, of a dirty-red colour, and a rotten (or almost friable) consistence.

The *chronic* variety of inflammation chiefly testifies to its duration by the presence of some one or other of the following peculiarities : — Its colour varies from pale red to dark brown or blackish red ; variations which are due to the exsudation being mixed with more or less of blood or pigment, as before alluded to. Its consistence is less regularly affected, but is often increased by a kind of hypertrophy. The exsudation is, on the whole, in smaller quantity; and of a less croupy or albuminous quality. And finally, it is exceedingly prone to pass into ulceration.

Concerning the inflammations of the various microscopic constituents of the mucous membrane, it must be confessed that our knowledge is at present very limited.

In most instances, the *villi* and *tubes* appear to share pretty equally in the disease. Of the two involutions of the mucous surface, however, the villi seem the most liable to suffer; a fact for which it would be easy, though scarcely justifiable, to assign a mechanical explanation. In some instances, the blind extremities of the gastric or intestinal tubes appear to suffer disproportionately, as compared with their upper extremities, and with the general surface of the canal. In such cases we may often see the capillaries around these blind extremities deeply injected, or their blood extravasated into the cavity of the tube; and in other instances, their natural cell contents may be seen exchanged for a dark softened granular mass. Precisely similar changes are often seen in the matrix of the tubes and of the villi; in which latter situation they are generally accompanied by a loss of the investing epithelium.

The closed *follicles* of the alimentary canal are the seat of various changes: some of which are obviously connected with an inflammatory state; while others probably have an equally definite, though less direct, relation to it.

An unusual number of these follicles seems to be one of their most frequent abnormal conditions. In such cases we may often find them strewn thickly through the submucous areolar tissue of the stomach, the small intestine, the large intestine, or even the entire alimentary canal.

But not only may it be doubted whether this increase in their number is due to an inflammatory process, but even whether it is a real occurrence. For in many instances there can be little question, that these follicles are not so much really multiplied in number, as revealed in increased numbers by their universal and extreme distention.

We have seen* that their apparent number varies greatly in different individuals; that, in children, they are generally very numerous and distinct; and that even that healthy afflux of blood, which obtains during the act of digestion, renders them unusually prominent and visible.

Hence it is to the presence or absence of other circumstances indicative of disease, that we must look for evidence as to the really morbid character of an increase in the number or size of these follicles. Wherever we find these alterations associated with a general dyscrasia, or with marks of congestion, hæmorrhage, or inflammation in the surrounding tissues, or with a change in the character of the contents of the follicle itself, there we are entitled to regard them as indicative of a morbid process. And conversely, where none of these appearances are present, we must be content to suspend our judgment on this point.

In typhoid fever, these follicles become the seat of a definite morbid process; which not only constitutes a specific element of the disease, but furnishes the pathognomonic lesion, which seems to dictate many of the details that distinguish the typhoid from the other varieties of fever.

The typhoid process in the intestine is almost limited to these follicles, of which it engages both the agminate and solitary varieties. Amongst the agminate follicles, those are most affected which lie nearest to the ilio-cœcal valve. The same rule applies to the solitary follicles, both in the small and the large intestine. In the latter segment of the canal, the change rarely extends beyond the follicles of the cœcum and ascending colon.

The process appears to commence by a stage of congestion or hyperæmia. This is at first general, and engages the whole mucous membrane of the lower part of the ileum. It subsequently increases in intensity, and at the same time becomes limited to the neighbourhood of the affected follicles; so that these are surrounded with minute rings of injected vessels, which are visible from the mucous surface, or can be seen gleaming through the transparent peritoneum as dark vascular points or streaks. The microscope traces this congestion into the small vessels (and especially the veins) which intervene between the several follicles.

The latter phase of congestion marks the access of the next stage: which corresponds to the exsudation and deposit of a new substance within the follicles, and (to a lesser extent) in the submucous tissue of their immediate neighbourhood. The infiltration distends the several follicles with a mass, which gives them a grayish, grayish red, or bluish-red colour; and a more or less firm or pulpy consistence. They thus acquire a thickness (1—2 lines) that raises them considerably higher than the adjacent surface, and causes them to stretch the mucous membrane above. Below, they rest on the muscular tunic. Of course the shape, extent, and situation of the follicles thus brought into view, is that of the original structures. Thus, in the case of the agminate follicles, we see an oval or elliptical patch that runs lengthwise along the free margin of the bowel. While in the solitary follicles, we find small round granules, of about the size of a millet seed, or a very small pea, irregularly scattered over the intestine.

The mass itself exhibits under the microscope, the ordinary constituents of the normal pulp of the follicle: mingled, however, with a variable quantity of blood; and with an amorphous granular substance in larger quantity, and of a browner hue, than natural.

The softening and breaking up of this pulpy mass constitutes the next stage of the change. In general, it occurs simultaneously over the whole of the agminate follicle: and thus detaches from the subjacent muscular tunic, not only the new deposit, but the follicles themselves; together with the areolar tissue by which they are connected to each other, and the tubes and villi of the mucous membrane by which they are covered. In other instances, the several follicles are softened and detached separately, or in clusters of two or three only; so as to leave some of the tubes and villi which normally occupy their intervals. In some cases, a portion of the patch undergoes a modified process; in which the contents of the follicle seem to make their exit through small openings at their projecting summit, with little or no disturbance of the adjacent tissues. Finally, in certain instances, more or fewer of the follicles are said to undergo a retrograde change, in which their contents undergo absorption, without either sloughing or dehiscence.

The removal of the new deposit leaves the characteristic typhoid ulcer; the shape, size, and situation of which are therefore precisely

* See p. 360.

indicated by the preceding description. The floor of the ulcer is formed by the muscular coat of the bowel, covered by a very thin stratum of areolar tissue. Its margin, somewhat irregular in outline, is a reddish or bluish-gray edge of mucous membrane: which was formerly raised and almost detached from the subjacent tissue by the distended and projecting follicles in its neighbourhood; but has now fallen down upon it, so as to form a perfectly flat, loose, and relaxed border, around the shallow ulcerated fossa of the patch.

In its further progress, the ulceration may extend in two directions. In the horizontal plane, it generally follows the shape, and rarely much exceeds the size, of the original patch. In the vertical plane, it may gradually destroy the muscular and peritoneal coats, and thus give rise to perforation. Such a deepening of the ulcer is accompanied by a narrowing of its width, so that the aperture in the serous membrane is generally of very small size.

The cicatrization of the ulcer, which follows the cessation of the local and general malady, takes place by the development of a firm, but very delicate layer of fibrous tissue, on the floor of the ulcer. This merges, by a gradual increase of its thickness, into the thickened margin before alluded to, where the original mucous membrane becomes intimately blended with the new fibrous cicatrix. The latter exhibits under the microscope the ordinary characters of this variety of fibrous tissue, and is generally covered by one or two layers of irregular flattened cells. The junction of the old and new structures is often marked by wrinkles and puckers, which appear to radiate from the new tissue of the cicatrix; and thus, as it were, measure and express its contraction. In very rare instances, this contraction gives rise to an obstruction of the canal. That it does not oftener do so seems due, not only to the limited extent of the ulcer around the bowel—an extent which scarcely ever exceeds $\frac{1}{3}$d or $\frac{1}{4}$th of its circumference—but also to the little injury generally inflicted on the textures subjacent to the ulcer, and to the amount and situation of the new tissue of the cicatrix. So little of this is deposited, and so exclusively is it limited to the surface of the ulcer, that the process of repair might almost be regarded as resulting in a mere condensation of those superficial layers of the original areolar tissue which are left intact by the ulcer.

The above series of morbid changes in the solitary and agminate follicles, is accompanied by a somewhat similar alteration in the lymphatic or mesenteric glands connected with the affected segments of intestine. This process closely resembles the preceding, except in the fact that it scarcely ever ends in the ulceration of the structures it engages. A stage of hyperæmia is soon followed by one of enlargement; the latter being due to the deposit of a substance, which gives to the glands affected, much the same grayish or reddish colour, and soft firm consistence, as that seen in the follicles. This deposit next undergoes a limited degree of softening: which is sometimes accompanied by hæmorrhage, rarely by suppuration, ulceration, or peritonitis; and is followed by its gradual absorption. The latter process slowly restores the glands to their normal size and colour.

Among the various inflammations of the different segments of the alimentary canal, there are only two to which we need accord any notice, apart from the general description as given above. These are, the gastritis produced by the ingestion of irritant (or rather caustic) mineral poisons; and the dysenteric inflammation which affects the large intestine.

In the *acute gastritis* caused by caustic substances, the stomach presents appearances of two kinds: — one, which forms a series of effects produced by the mere chemical action of the poison on the tissue, and which might therefore be to some extent imitated by introducing it into the stomach of a newly killed animal; and another, which represents the subsequent vital reaction of the tissue against the poison, constituting the phenomena of inflammation, properly so called.

The first of these will of course vary, not only with the nature of the poison, but also with a variety of other circumstances; especially with its quantity, concentration, and solubility, as well as with the amount and duration of its contact with the stomach. Thus according to the nature of the poison, the organ may either undergo softening and solution, or hardening and coagulation; may either be blanched, or carbonized; coloured, or deprived of its colour; swollen by an imbibition of fluid, or contracted by the loss of its own water of composition.

The second or inflammatory class of appearances will necessarily depend upon the extent in which the first preceded them; since it is chiefly in the tissue beneath the destroyed part, that the reactive inflammation is set up. Thus if the epithelium be the only structure which has been acted upon by the poison, it is soon replaced by the development of a new layer in the exsudation poured out; a process which implies but a moderate hyperæmia, and leaves no traces in the structure of the part. While, if the direct action of the poison involve all the coats of the organ, it may give rise to a more or less extensive (and generally fatal) perforation.

The intermediate degrees of this action are followed by a set of appearances which, with great differences in particular poisons and individual cases, may be summed up as follows. The vascular changes consist chiefly in the production of an intense congestion or hyperæmia. The blood-vessels thus injected communicate to the mucous membrane a colour which takes every conceivable shade, from intense red to almost black. In the latter case, the microscope will often show that the blood is coagulated within the vessels, and here and there forms patches of hæmorrhage externally to them. The exsudation which accompanies this congestion, renders the mucous membrane swollen, soft and relaxed; — a change which is generally due to the interstitial effusion of a large quantity of bloody serum. A similar fluid is also poured out into the interior of the organ in variable quantity; and its effusion is generally attended with the detachment of the sloughs previously caused by the direct action of the poison. The exsudation also often distends the submucous areolar tissue, so as to separate the muscular and mucous tunics from each other. Sometimes the former of these two tunics is only rendered paler and more yielding than natural. But in other cases, the whole parietes of the organ ultimately become converted into a rotten, brown, or reddish mass, in which scarcely any structure is distinguishable.

The details of those changes by which the moderately inflamed gastric membrane returns to a healthier state, are equally variable with the preceding. The separation of one or more flat sloughs lays bare what may be regarded as an ulcerated surface. The establishment of suppuration on this surface precedes the formation of the reparative tissue. When fully developed the latter substance exhibits the ordinary fibrous structure of cicatrix. And since the process of exsudation previously extended to some little distance from the ulcer, the margin of the cicatrix blends gradually with the surrounding healthy mucous membrane; while its base generally exhibits similar gradations of structure with the subjacent tissues. The subsequent contraction of the new tissue may materially alter the shape of the organ, and diminish its size. Indeed, where there has been much loss of substance at one point, it may even cause a more or less complete obstruction or occlusion of its cavity.

In *dysentery*, although the morbid changes appear to begin in the follicles, and often predominate here, still the relation of these structures to the process is far less intimate and specific than in typhoid fever. The dysenteric state may rather be regarded as an intense inflammation of the whole of the mucous membrane; which engages these closed sacs with a rapidity and severity that seem to be not more than proportionate to their vascularity, and to the facilities which, as it were, their very construction offers to the exsudative process.*

The morbid appearances chiefly affect the large intestine; and generally exhibit an increase in severity from the cœcum towards the anus. In a subordinate degree, however, they not unfrequently involve the adjoining segment of the ileum.

The process begins as an enlargement of the solitary follicles of particular parts of the bowel, which is quickly followed by appearances of inflammation in the adjacent mucous membrane. Red, swollen, and injected streaks are seen occupying the most projecting parts of some of the transverse folds of the bowel. And on examining these streaks, we find that the epithelium is here and there raised from the subjacent tissues; either as a grayish flake, or as a semi-transparent vesication enclosing serum. Beneath this cell-growth is the raw and denuded mucous membrane; which is softened, reddened, and infiltrated (especially in its submucous areolar tissue) with a bloody serum, that easily exsudes on making pressure. The above change soon extends, from these isolated streaks, to larger portions of the mucous surface; so as to involve, not only the projecting folds of the bowel, but also their intervening depressions. The detached epithelium, which has a dirty gray colour, becomes mixed with the subjacent reddish exsudation. The latter is generally thick and glutinous: but is sometimes of a denser and more croupy consistence; which permits it to be detached and expelled as a more or less perfect cast of the inflamed segment of the bowel. The mucous membrane itself acquires a pale, or dirty-red, or even somewhat yellowish, colour; as well as an increased thickness, and a pulpy gelatinous consistence. The submucous areolar tissue beneath it also becomes infiltrated with an exsudation that has the characters of bloody serum; its enlarged follicles ulcerate or rupture; and its interstices are here and there raised by effusion into protuberances, which give a mammillated aspect to the free inner surface of the intestine. In extreme cases, these projections multiply, enlarge, become confluent, and thus proportionally thicken the whole texture.

These changes are usually accompanied by a more or less considerable dilatation of the intestine; the cavity of which contains, in addition to a large quantity of gases, a mixture of fæces, blood, epithelium, and lymph, in variable proportions.

An increase in the intensity of the above appearances rapidly converts the inflamed membrane into a sloughy or mortified mass. Prior to this event, it becomes dark red, brown, or almost black, from congestion and extravasation of blood. Where less ecchymosis is originally present, and the blood poured out undergoes alterations after its effusion, it frequently offers a dirty gray or almost greenish colour. Subsequently to the separation or dissolution of the sloughy membrane, the denuded submucous tissue may be seen occupied by black masses of altered and coagulated blood, and by more or fewer of the vascular trunks formerly distributed to the destroyed tissues. And at this stage of the process, if not previously, the adjacent muscular and peritoneal coats exhibit every evidence of their sharing in the disease. The former becomes infiltrated with blood, or serum, and of a dark, gray, or ash-coloured hue. While the peritoneum loses its smooth and shining appearance, acquires a dirty reddish colour and an injected state of its vessels, and often has its surface visibly occupied by a more or less purulent or sero-purulent exsudation. In extreme cases, these changes bring about an adhesion of the diseased bowel to neighbouring segments of

* See p. 357. *et seq.*

the large or small intestine. The lymphatic glands connected with the diseased intestine are also altered; becoming swelled, injected, and of a red or bluish-red colour. These alterations seem chiefly due to their irritation.

The changes by which the diseased portions of intestine are restored to a healthier state, of course vary with the intensity of the process, and with the extent to which it has proceeded. Thus, in slighter cases, the process is one of mere resolution. While, after the occurrence of sloughing and loss of substance, the reparative act is much more imperfect. It is effected by the development of a cicatrix; which is gradually formed in the suppurating ulcer that is left by the detachment of the gangrenous portion of membrane.

This cicatrix, though similar in structure to that noticed in the typhoid process, is very different both in its amount and arrangement. Its smooth (and apparently serous) surface often has to fill up the intervals of the irregular islands or isthmuses of mucous membrane which are left by the process of sloughing; and hence the latter are often seen as thick projecting nodules, surrounded by a basis of new tissue. The base of the cicatrix extends to a variable depth in the subjacent coats of the bowel; and, in chronic cases, often forms a thickened base, that sustains an ulcer of long standing and variable size. Finally, the great loss of surface which the cicatrix replaces, concurs with the two preceding circumstances to render its subsequent contraction of great influence on the shape and diameter of the bowel. Thus the ordinary situation of the sloughs in milder cases — on the projecting folds of the mucous membrane — seems at least a partial explanation of the frequency with which the contracted cicatrix takes the form of a cord or fold, itself more or less transverse to the axis of the tube, and hence very liable to cause obstruction of the canal.

Ulceration constitutes a frequent termination of the various inflammations of the alimentary canal. In this tube, as in most other parts of the body, it is associated with inflammation, chiefly as a secondary result; which is conditionated, not so much by mere intensity of the process, as by a certain slow and chronic rate of its progress. Thus in many of the abnormal conditions already alluded to, the sloughing occasioned by rapid and violent inflammation is often replaced by this interstitial mode of destruction, during the subsidence of the earlier and more acute symptoms. While, in milder and more chronic cases, it occurs independently of the gangrenous process. How far it is due to the vascular disturbance which inflammation produces; or to the direct effects of the exsudation; or finally, to a mere increase of the ordinary destructive absorption, or a decrease of assimilation; — it would be irrelevant to this sketch to inquire.

The specific ulceration of typhoid fever has already been mentioned, as well as the secondary ulceration to which it often gives rise. The ulceration of tubercle and of cancer of the canal will be hereafter alluded to; as being essentially due to the metamorphosis of certain deposits in the tissues of the organ, and to the reaction excited in the latter by their presence. Hence we need here only enumerate one or two of the remaining forms of ulceration most frequently seen in the stomach and intestines.

It is but rarely that we find ulcerations of the tube which can be attributed to mechanical causes.

In certain instances, however, the mere pressure of a neighbouring tumour, or of some diseased viscus, results in this process. But in such cases, the access of ulceration is usually preceded by the occurrence of exsudation and adhesion, which limit the amount of original substance it removes, and thus to some extent obviate the danger of its perforating the walls of the tube.

The impaction of solid masses in the canal more frequently leads to such a result. In rare instances, these masses find their way into the canal from neighbouring organs; as is the case with gall-stones. In still rarer cases, they seem to be formed solely by the concretion of the liquid contents of the canal; resulting in intestinal calculi. In most instances, however, they are due to the introduction, from without, of various foreign bodies; such as cherry-stones, pins, needles, or nails. In all cases, the ulceration depends, not only on the size, but also on the shape and surface, of the mechanical irritant. The most familiar examples of such ulceration are seen in the vermiform appendix: where it is not uncommon to find perforation produced by an impacted mass; which, on examination, proves to be some one of the small solids just alluded to, encrusted with rough calcareous matter, that has been derived from the contents of the canal.

Ulcer of the stomach.—In the stomach and the first portion of the duodenum, the ulcerative process is often present in a peculiar form: namely, that which is usually called the simple or perforating ulcer. Of these two epithets, the first refers to the slight appearances of inflammation often present in the neighbourhood of such ulcers; the last, to the frequency with which they extend to such a depth, as to perforate all the coats of the organ.

The size of these ulcers varies from that of a fourpenny piece, to that of a crown piece, or even larger. Their shape is usually circular; sometimes elliptical: occasionally, however, more irregular. In some instances, this irregularity of outline is due to the fusion of two or more neighbouring ulcers into one, by an extension of their adjacent margins. But in a majority of cases, only single ulcers are present.

The ulcer is generally situated, either in the neighbourhood of the pylorus, or near the lesser curvature of the organ: more rarely in front than behind; and least frequently of all, in the cardiac sac.

The mucous membrane in the neighbourhood of the ulcer is sometimes a little swollen: and the immediate margin of the excavation is often indurated and raised above the level of the adjacent mucous surface. But it offers no other appearances worth mentioning as indicative of inflammatory reaction in the contiguous tissues.

The mode in which the ulcer penetrates the various tissues is somewhat characteristic. The smooth, sharp and vertical edge by which it passes through the mucous membrane, and reaches the submucous tissue, is here exchanged for a less regular one; which forms a circle of smaller diameter than the opening in the mucous coat. In like manner, when the ulcer has gradually eaten its way through the muscular coat, it reaches the peritoneal coat, at a point which about occupies the centre of this smaller circle. Hence, the whole depth of the ulcer forms a cone; the base of which is at the free or internal surface of the stomach, while its apex occupies the peritoneum. The latter membrane is scarcely ever destroyed by mere ulceration, except in those instances in which it has previously been strengthened and defended by an exsudation of lymph. Where this has not been deposited, the peritoneum becomes converted into a yellow slough; the rupture or detachment of which gives rise to perforation of the stomach, and allows its contents to escape into the abdominal cavity.

The process by which the gastric ulcer originates is at present unknown. Rokitansky thinks it probably begins as a hæmorrhagic erosion, or a circumscribed slough; and that it gradually extends by its basis throwing off a succession of laminated sloughs, or exfoliations. Some such process he has indeed observed in a few instances. On the other hand, if we may venture to regard that ulcer of the duodenum which sometimes occurs in severe burns, as analogous to the gastric ulcer, we should probably find reason for concluding, that the ulcerative process may sometimes occur, without being preceded by hæmorrhage, sloughing, or any appreciable exsudation, in the situation of the affected part.*

The cicatrization of such ulcers may take place at almost any stage of their course. The precise details of its occurrence vary with the amount of destruction which has preceded it. Where the destructive process has been limited to the mucous membrane, there is little more than a condensation and thickening of the subjacent areolar tissue; which ultimately forms a scar that has a shape similar to the ulcer. But where the muscular coat has been partially destroyed, its remaining lamina, and the subjacent peritoneum, are generally more or less folded or crumpled up, so as to bring the margins of the ulcer nearer to each other. Hence the resulting cicatrix has a much more irregular form; and often contracts into a kind of thickened cord, with radiating extremities, which seriously affects the shape and diameter of the whole organ. The amount of contraction thus impressed upon the stomach varies, other things being equal, with the size and shape of the ulcer.

The extension of the ulcerative process would always end in perforation, were it not this event is, in most instances, to some extent guarded against by the occurrence of adhesion. From what has been already stated, it is evidently very doubtful whether the ulcer originates in an inflammatory state. And in many cases, it certainly seems devoid of all the ordinary appearances of inflammation during its progress. But it is often accompanied, not only by swelling and induration of its mucous margin, but by exsudation and hardening at its base, and by adhesive inflammation of the neighbouring tissues. Thus the peritoneal coat at the bottom of the ulcer becomes inflamed, and pours out upon its free surface a stratum of coagulable lymph; by means of which the stomach may become united to any adjacent viscus. In this manner the liver above the organ, or the pancreas behind it, may become attached to the outer surface of the stomach, at a point corresponding to the situation of the ulcer in its interior. But the more mobile diaphragm and anterior wall of the belly are less frequently the seat of such adhesions.

The adhesion does not, however, replace the loss of substance in the gastric coats. And hence, in many of these cases (just as in adherent wounds of the stomach, attended with much loss of its parietes) the mucous membrane around the edges of the ulcer becomes prolapsed and protruded into it; and thus comes into contact with the surface of the adhesion at its base. The substance of the adhesion itself may either ultimately become converted into a cicatrix: or it may be gradually drawn out by the constant traction which the stomach exercises; so as to form a hollow funnel-shaped tube, that is lined by a smooth surface having the appearance of a serous membrane.

The efficiency of the adhesion, as a means of protection against perforation, varies with its situation, and still more with its structure. Where it is a mere thickening of a delicate fibrous network by inflammatory lymph, as is generally the case when it occupies the omentum, it is of little avail in this respect. While where the exsudation possesses a fibro-cartilaginous character, such as is often seen in the adhesions which unite the stomach with the liver, it forms a much more efficient protection against such an event.

But in many instances, a continuance or renewal of the ulcerative process attacks and destroys the new tissue itself: and either penetrates the viscus (pancreas, liver, or spleen)

* See Pathological Transactions, vol. i. p. 258, for an instance brought forward by Mr. Prescott Hewett; where one of these ulcers seemed to be commencing as "a slight depression in the surface of the mucous membrane, which in their neighbourhood presented some traces of increased vascularity."

to which this is attached; or, by extending laterally, and opening into the peritoneum beyond the margin of the adhesion, leads to perforation.

Hæmorrhage to a considerable extent generally occurs at some stage or other of the ulcerative process. In the earliest periods of the ulcer, this hæmorrhage seems to proceed chiefly from smaller vessels. But after the coats of the stomach have once been penetrated, the larger vessels which run on its exterior surface become very liable to be attacked, eroded, and laid open. The hæmorrhage thus produced is a frequent cause of death in this disease. The peritonitis produced by perforation is, however, still more frequently fatal.

Lientery.—A peculiar ulceration of the follicles of the large intestine has been described by Rokitansky, under the name of *lientery.* Like other ulcerations of this segment of the canal, diarrhœa is a constant symptom of its presence. The process begins by a distention of the follicles, which is accompanied by a dusky-red injection of the vessels on and around their summits. The contents of the follicle next suppurate ; and are discharged from the resulting "follicular abscess," through an ulcerated or ruptured opening in the summit of the follicle itself. The follicle thus emptied is next removed by a process of ulceration ; the limits of which subsequently extend, so as to form a round or oval ulcer, which has the size of a pea or a small bean. The mucous membrane at the margin of these ulcers is relaxed; and of a pale, grey, or livid colour. And the cellular tissue which forms their base exhibits similar appearances, which are sometimes combined with the various results of slight extravasation of blood.

The subsequent enlargement of these ulcers in various directions, and the fusion of several into one which may thus be brought about, constitute a secondary ulcerative process, which often lays bare a large surface of the submucous or muscular coat. The bases of these irregular secondary ulcers present characters like those of the primary ulcers just mentioned. Like the dysenteric process, this follicular ulceration increases in intensity from the cœcum onwards towards the rectum. And in acute cases, it sometimes extends upwards into the ileum.

Hypertrophy.—The *hypertrophy* generally described by authors as one of the abnormal conditions of the intestinal canal probably includes, under one name, a variety of states ; which differ widely from each other, both in their nature and results.

(1.) That thickened state of the tunics of the tube which is generally found behind an obstruction of gradual origin or long standing, is the best (if not the only) instance, to which we can really apply the word hypertrophy ; in its strict sense of an excessive nutrition of tissue. Here the propulsive powers of the tube have to struggle against the increased resistance which is offered by the constricted or obstructed part : and this increased activity results in an exalted nutrition of the unstriped muscular fibres, which materially adds to their bulk. Such a true hypertrophy of the muscular coat may be seen in certain cases of simple stricture of the rectum or œsophagus. And a similar condition is not unfrequently associated with the scirrhous constriction of the pylorus; as a moderate hypertrophy of this tunic over a large part of the stomach.

But a careful examination into the minute anatomy of this hypertrophy would generally show, that it can hardly be regarded as due to a mere exalted nutrition of previously existing tissues. On the contrary, even in those instances in which it appears, to the naked eye, almost limited to the circular fibres of the muscular coat, the microscope often reveals evidence of a more extended change. The neighbouring submucous areolar tissue is always infiltrated with an exsudation, in larger quantity, and of more gelatinous consistence, than the nutritional fluid proper to the part. The partitions of areolar tissue by which the bundles of the unstriped fibres are normally separated from each other, are increased both in solidity and bulk. And, finally, the fibre-cells themselves not only present a more variable, as well as a generally increased size; but are in many places surrounded by a more or less perfect layer of what seem to be developmental forms of these structures.

(2.) In other cases of what is often called hypertrophy, a more partial and imperfect process of the same kind appears to take place, incidentally to the exsudation of a plasma, which may doubtless be referred to an inflammatory origin. In such instances, an examination of the tunics of the canal generally shows all of them to be more or less infiltrated with a proteinous substance ; which renders them much thicker, whiter, and more resisting than natural. Mingled with this deposit, we often find an unusual quantity of the unstriped muscular fibre. But it is not always easy to verify the exact amount of true muscular hypertrophy that has taken place. For the exsudation, which generally predominates in the submucous and subserous coats, has also a great tendency to involve the fibrous sheaths of the various bundles of the unstriped fibres; and is thus capable of communicating to the muscular coat an increased thickness, which by no means implies a proportionate hypertrophy of its characteristic fibres.

The author is inclined to conjecture, that, in these instances of interstitial exsudation, the muscular fibres are capable of being affected in either of three ways. In some instances they seem to be really hypertrophied ; a process which is possibly the indirect result of the immovable and thickened condition of the tube, being such as to demand increased contractions, and stronger muscular structures, in order to effect its various movements. In a second class of instances, they seem to be but little affected. Finally, in others — and especially in those cases in which the copious exsudation has subsequently contracted, so as to diminish the calibre of the tube,— the muscular fibres themselves seem to undergo a process of atrophy, which ends in their complete disappearance.

(3.) The above remarks may serve to illustrate a brief allusion to a third (and very frequent) variety of what is called hypertrophy of the digestive canal, in which it is still more difficult to determine the exact change that has taken place. In these cases an albuminous plasma exsudes into the coats of the canal: either pretty equally throughout; or with a more or less marked preference for the submucous or subserous areolar tissue, and with marks of inflammation in the neighbouring mucous membrane or peritoneum respectively. When examined under the microscope, this albuminous plasma generally exhibits all the appearances which attend the abnormal development of fibrous tissue. But the fibres thus developed as the product of a diseased (and often an inflammatory) action, offer marked differences in their structure and arrangement from those of the normal areolar tissue among which they originate. While, as regards the changes undergone by the latter or healthier texture, it is often impossible to decide whether it has been augmented or hypertrophied; or whether it has not rather experienced such an interference with its nutrition, and such a loss of its substance, as amounts essentially to its atrophy.

Polypi.—The tumours which have received the name of polypi agree in the common character of projecting into the cavity of the digestive canal, by means of a peduncle or stalk of variable length, that attaches them to its walls. Their size varies from that of a pea to a pigeon's or hen's egg. They are almost always covered by the mucous membrane: in the submucous areolar tissue beneath which they appear to be generally formed.

It can scarcely be doubted that the shape of these polypi — like that of the papilliform tumours on the external integuments — is sometimes determined by a definite arrangement or development of the plasma out of which they are constructed. It is, perhaps, chiefly in this way that isolated malignant growths under the mucous membrane so frequently assume the pedunculated or polypoid form. But it seems certain that, in many instances, their form is partly the result of a mechanical traction, such as the muscular contractions of the alimentary canal itself might exercise on almost any small tumour projecting from its mucous surface. The pedicle* of the tumour is thus continually drawn out and lengthened. And the intussusception of that segment of intestine from which this pedicle arises, sometimes affords a remarkable testimony of the mechanical activity of the bowel.

The interior of the non-malignant polypiform tumours generally consists of a more or less completely developed fibrous tissue. In some cases, however, they contain a mass of adipose tissue, which causes them to resemble appendices epiploicæ. In very rare instances, their contents approach the amorphous character, and friable consistence, of a tuberculous deposit. And finally, they sometimes constitute true mucous polypi; which are distinguished by their lobulated form, their great vascularity, and their erectile and dilatable texture.

The various small tumours which occasionally occupy the submucous tissue of the bowel scarcely require any separate description. Cysts are comparatively rare in this situation. Fibrous, or fibro-cartilaginous masses are less infrequent. The latter rarely become the seat of a process of true ossification. The inorganized earthy matters oftener found in their interior are formed, either by obsolete tubercle, or by the cretified contents of old abscesses, the pus of which has undergone a partial absorption.

Tubercle. — The digestive canal is more frequently the seat of tuberculous deposit than any other organ of the body, the lungs only excepted. The pulmonary tubercle is, however, far more frequent than the intestinal. And the latter is not only generally preceded by the former; but is rarely seen to any extent, before the tuberculous matter deposited in the lungs has already reached the stage of softening and suppuration.

The different segments of the canal are affected by it in the following order of frequency: the lower part of the ileum; the cœcum; the large intestine generally; the upper part of the ileum; the jejunum; the duodenum; and (very rarely) the stomach.

Both forms of tubercle are met with in the intestinal canal. In a vast majority of instances, none but the crude, yellow, or caseous tubercle is detected. But in cases in which the disease has taken an unusually chronic course, the grey granulations are sometimes met with. The latter appear gradually to assume the caseous form; the change beginning at their centre, and extending thence to their circumference.

The deposit usually begins by engaging the agminate and solitary follicles of the lower third or half of the ileum; filling and distending their cavities with crude tubercle. A marked (and often intense) redness of this segment of the bowel usually accompanies the deposit; and remains, as a more or less distinct hyperæmia, during the remaining stages of the process.

The caseous tubercle contained in these follicles next undergoes the process of softening. The summit of the sac bursts or ulcerates; and its contents escape into the cavity of

* The movements of the intestines upon each other often seem to exert a similar mechanical influence on tumours or deposits attached to their peritoneal surface.

the canal. The follicle itself is thus either evacuated or destroyed: and its situation is then occupied by a small excavated ulcer, varying in size from a millet-seed to a pea.

This primary ulcer now becomes the seat of a process of secondary ulceration, which extends its size in the two directions of width and depth. Its superficial extension causes several of the small primary ulcers to become fused into one; and sometimes widens the resulting secondary ulcer, so as to form a patch of ulceration that more or less encircles the bowel. Its vertical progress successively engages the submucous and muscular coats, and thus finally reaches the peritoneum. The latter membrane, if not strengthened by the lymph of adhesive inflammation, now sloughs or ruptures; with the result of a fatal perforation.

This extension of the ulcerative process, and the means by which it is effected, together constitute the chief characteristics of tubercular disease in the intestinal canal: and render the loss of substance it brings about in the walls of this tube, strictly analogous to that by which it excavates the tissues of the lung. The base and margins of the tuberculous ulcer have a ragged swollen appearance; are surrounded by a gelatinous infiltration; and are themselves the seat of an interstitial deposit of cheesy tubercle. The softening of this deposit, and the suppuration of the original tissues in which it is entangled, continually increase the size of the ulcer; and the inflammation thus produced tends as continually to increase the deposit of new tubercle. Hence the tuberculous ulcer assimilates, so to speak, the adjacent tissues to itself: and is never bounded by healthy or heterogeneous tissues; like those which adjoin the gastric ulcer, or the specific follicular ulcer of the typhoid process.

As the tubercular ulceration extends, the intervening submucous tissue, even where hitherto healthy, generally becomes the seat of a similar deposit and destruction. Hence, in well marked instances of acute intestinal tuberculosis, these ulcerations occupy a large proportion of the affected surface of bowel; leaving only small insulated patches, or fungous projections, of the original mucous membrane. And in extreme cases, they may even remove this tunic from a large continuous segment of the bowel.

The cicatrization of such ulcers is rarely seen, except in cases where the process has ceased in one part, while it has still been going on in another. In such instances, the removal of the softened mass already present ceases to be followed by any further interstitial deposit of fresh tubercle in the margin of the ulcer; and a plasma, which exsudes on the bare and ulcerated surface, is ultimately developed into a cicatrix of the ordinary structure and appearance. The subsequent contraction of this cicatrix is of course proportional to the loss of substance which it has had to replace. The zonular direction of the previous ulcer often gives it a form more or less approaching that of a cord or imperfect septum; which lies transversely to the axis of the tube, and materially narrows its calibre. In rare instances, the cicatrix contains fragments of the cretaceous or other varieties of obsolete tubercle.

Cancer. — Cancer affects the intestinal canal under all three of its chief forms; namely, scirrhous, medullary, and colloid or areolar cancer. And even its villous and epithelial varieties are occasionally present. The latter is, however, very rarely met with.

In most instances the cancerous growth is at first seated chiefly in the submucous areolar tissue; from which it gradually advances towards the inner and outer surface of the canal, so as ultimately to involve the whole of its coats. But the three forms of cancer fall with various degrees of intensity on different parts of this areolar layer. The scirrhous variety begins in its deepest stratum; and in those fibrous septa of the subjacent muscular bundles which are connected with it. The areolar or colloid variety chiefly affects the middle and looser laminæ. While the medullary and the villous variety generally occupy the immediate neighbourhood of the basement membrane of the mucous tunic. Finally, in the epithelial variety, there seems to be a definite metamorphosis of all the histological elements of the mucous membrane itself.

Those rare instances in which the cancer seems to begin in the subserous areolar tissue are in reality cases of cancer of the peritoneum; which membrane they almost always involve in its visceral reflexions (omentum and mesentery), as well as in some parts of its parietal laminæ.*

The cancerous growth is generally primary; but is sometimes secondary to a deposit in some neighbouring organ. In the latter case, the intestinal canal may either be involved by a mere extension of the disease from absolute contact; or it may be affected through the intervention of the lymphatic glands and vessels. The first of these contingencies may be illustrated by the way in which the stomach is sometimes involved in a cancerous tumour of the liver: the second, by the far more numerous instances, in which the large intestine becomes cancerous, as the result of similar disease occupying the neighbouring lymphatic glands.

The above varieties of the cancerous growth occur with very unequal frequency. The scirrhous is by far the most common, the medullary less frequent, and the colloid or areolar rarest of all. And while the former is usually primary, the two latter are more frequently secondary; or are often admixed, in varying proportions, with what was originally a scirrhous growth. In the latter instances, the scirrhus is sometimes said to have undergone a transformation into medullary cancer.

* Compare Art. PERITONEUM.

But it is very rarely, if ever, that such a metamorphosis really occurs. In general the process thus designated consists merely in the deposit of new cancerous matter within, and especially around, the scirrhous mass; and not in any true metamorphosis of the latter growth itself.

The cancerous disease of the intestinal canal is often associated with the existence of a limited amount of hypertrophy. For the deposit of scirrhus in the coats of the canal not only thickens and hardens their substance; but, by the annular form it affects, has a special tendency to obstruct the calibre of the tube. Where it does this slowly, and with little disturbance of the general health, the obstruction is often partially compensated by a true conservative hypertrophy of the muscular coat behind the diseased part. But, for similar reasons, this hypertrophy is often associated with dilatation: — an alteration which is indeed sometimes carried to an enormous extent; so that the stomach, for example, fills almost the whole abdominal cavity.

Of the various morbid conditions already alluded to, there is only one which is very liable to be mistaken for cancer; namely, that fibrous thickening of the gastric and intestinal parietes which is usually termed hypertrophy. This state offers so many points of resemblance to the scirrhous deposit, that it seems worth while to enumerate the chief points of contrast between them. Of these we will only premise that, though they generally afford ample materials for a satisfactory decision, they occasionally leave us in great doubt as to the fibrous or scirrhous character of the particular specimen under examination.

Comparing these two states in their ordinary form, as seen in the stomach, we may sum up their chief differences as follows:— 1. The scirrhus affects the submucous tissue in a greater degree than the hypertrophy, which is more evenly distributed throughout the three coats. 2. The scirrhus often presents a similar irregularity of distribution in the horizontal plane of the gastric coats themselves, which it thus renders uneven and protuberant; while the hypertrophy forms what is generally a larger and more uniform expanse. 3. The appearance of the scirrhus is white, hard, and gristly or cartilaginous; that of the hypertrophy is yellower, tougher, and more elastic. 4. The muscular substance is involved in hypertrophy chiefly by the atrophy or enlargement of its bundles, within their thickened cellular sheaths. But in scirrhus, it undergoes a characteristic metamorphosis; by virtue of which its structure may almost be * said to approach that of colloid cancer. The fibrous septa become the seat of a development of new fibres; while in their loculi or intervals, the muscular fibres are replaced by a reddish-yellow gelatinous substance, which consists of characteristic cancerous cells, in various stages of development. 5. The scirrhus fuses and confounds the various tunics; which, in the hypertrophy, generally remain tolerably distinct. 6. In scirrhus, ulceration is of more frequent occurrence, of earlier access, and of wider extent, than in hypertrophy. 7. In scirrhus, the neighbouring glands and organs generally become at length affected by an enlargement and deposit, which itself partakes of the cancerous characters. 8. The microscopic characters of the two morbid products are usually decisive; the scirrhus almost always offering the cell-forms characteristic of cancerous growth, in some part or other of its mass. Thus, for instance, even where the fibres of the central and cartilaginous substance are so numerous and well-developed as to obscure the cells they involve, the gelatinous matter enclosed within the meshes immediately around this harder mass will generally yield an abundant cell-growth; or the still softer periphery of the tumour will afford the unmistakable cells of medullary disease.

* Marked specimens of this kind are, I believe, sometimes mistaken for the rarer true areolar cancer.

Of the various segments of the digestive canal, the stomach is by far the most frequent seat of cancer. The large intestine stands next to it in liability to this disease, the liability diminishing successively from the rectum through the sigmoid flexure, to the remainder of the colon. In the cœcum, however, it seems somewhat increased. The small intestine is very rarely affected, except in acute and general cancerous cachexia; in which the mucous membrane, and its submucous tissue, are sometimes infiltrated with medullary deposit in the situation of the agminate follicles.

In the *stomach*, cancer generally occurs as a scirrhous deposit which surrounds the pyloric extremity of the organ. The cancerous growth is strictly limited towards the duodenum, by the pyloric valve; but it extends a variable distance along the right side of the organ, generally favouring the lesser curvature. The neighbouring gastric surface is often occupied by small isolated deposits of cancerous matter, which lie beneath the mucous membrane. And the healthy muscular coat, as before mentioned, is also frequently hypertrophied over a large extent of the same locality.

The chief peculiarities of the scirrhous mass have been enumerated in speaking of the differential diagnosis between it and hypertrophy of the stomach. Beginning in the submucous tissue, and the subjacent muscular coat, it rapidly involves both of these structures in a white cartilaginous-looking mass; the more opaque and fibrous parts of which often seem to give off bundles of fibres, that pass completely through the muscular coat. The anatomy of these fibrous bundles has already been mentioned. The disease advancing, involves the subserous tissue and the peritoneum, on the one hand; and the mucous membrane on the other. The latter of the two extensions is generally both earlier in date, and more considerable in amount. After the disease has thus fused into one mass the muscular and mucous coats, the distention and vascular disturbance undergone by the latter gradually effects its disorganization. Its epithelium becomes detached; its surface ulcerates or sloughs; and more or less hæmorrhage is excited. At this time, if not before, the cancerous process is generally so far modified, as to give rise to the deposit of the medullary instead of the scirrhous variety. The eroded surface of the tumour thus becomes the site of a bleeding fungous growth; the hæmorrhage from which, more or less altered by the fluids of digestion prior to its being ejected from the stomach, gives rise to the characteristic coffee-coloured vomiting which is almost always present in the latter stages of the disease. The metamorphosis of the cancerous mass is generally followed by sloughing or ulceration, either of which may end in the perforation of the organ. But this event is sometimes prevented by the adhesion of the peritoneal surface of the stomach to neighbouring structures; and is, perhaps, still more frequently staved off by the continuous deposit of new cancerous matter beneath and around the ulcerating mass. The perforation of the gastric parietes may give rise to an abnormal communication between the stomach and some neighbouring segment of the canal:—for example, the transverse colon, or some part of the small intestine. Or it may even open on the exterior of the belly; or penetrate the thoracic cavity.

The medullary form of cancer, which is not unfrequently seen as a secondary deposit at the surface and margins of the scirrhous mass, sometimes occurs independently, as a continuous or discrete deposit in the submucous areolar tissue. It offers its ordinary characteristic structure and appearance.

The areolar form is also more frequently secondary than primary. It is by no means uncommon to find the hard scirrhous texture of the centre of the cancerous pylorus merge into a fibrous network as it approaches the inner surface of the organ; — a network the large meshes of which are filled with a gelatinous mass. The fibres which constitute these meshes are generally long, pale, and extremely delicate; and their narrow outline is here and there bulged by persistent developmental cells. The gelatinous mass which they enclose consists of cells, which are often large and compound; sometimes caudate, or pigmentary. It is possible that this structure is to some extent produced by a true metamorphosis of the previous scirrhus: its fibres being multiplied, at the same time that they are enlarged and distended by the deposit, between and amongst them, of a soft mass of cells. In some instances we find evident traces of a development of new fibres, which gradually break up the primitive loculi into secondary cells. The most superficial or internal of these loculi project from the mucous surface into the cavity of the stomach; where they often become the seat of a medullary or fungous growth, which undergoes ulceration and hæmorrhage.

Stricture of the intestine. — The most frequent cancerous affection of the large intestine is a scirrhous deposit, which more or less encircles the tube. The extent to which it passes round the circumference of the canal is determined chiefly by its primary or secondary nature. In the former case, it is a complete circle. In the latter case, it generally forms but part of a circle; and occupies that side of the intestine, which is nearest to the gland or other neighbouring texture, from which the disease may have been derived.

In either kind of scirrhous stricture, the deposit may subsequently extend, for a variable distance, in the direction of the length of the canal. But so long as it remains limited to a simple annular mass of gristly scirrhus occupying the submucous tissue, its chief effect is that of narrowing the canal. The influence of this narrowing on the neighbouring segments of the bowel is at first merely the mechanical obstruction which it offers to the transit of the intestinal contents. Where this obstruction amounts to a complete occlusion, it is speedily fatal: the intestine above the stricture becoming enormously distended by its contents; and undergoing inflammation, gangrene, or even rupture, as the result of this distention. A slower process of constriction, or a less complete obstruction, generally give rise to a combination of a similar dilatation, with a variable degree of hypertrophy; the latter change being often carried to such an extent as greatly to increase the thickness of all the coats of the bowel, and especially of the muscular tunic.

The obstruction is often increased by the way in which the diseased part of the intestine becomes abnormally united with neighbouring viscera or walls of the belly. In the secondary form of scirrhus, the mass is of course attached and fixed, almost at the very commencement of the process of deposit. But in the primary form, it may remain free until a comparatively late period of the disorder; when the weight of the tumour often causes the bowel to gravitate into a more or less unnatural position. In either case, its occurrence often alters the course of the canal, by bending it at an acute angle opposite to the adherent part. The bowel is thus placed at a still further disadvantage for the transmission of its contents.

The subsequent progress of the disease requires little notice. The growth of a medullary fungus, or the deposit of a colloid or areolar mass upon the surface of the ulcerated stricture, may of course increase the obstruction which the latter produces. Or, conversely, its sloughing or ulceration may restore the permeability of a previously almost occluded canal. Finally, the extension of the disease upwards, into the dilated segment of intestine above the stricture, may convert this part into a large receptacle, which is bounded by thick and solid cancerous walls. Where the lower outlet of this cavity remains patulous, life is sometimes preserved under such an unfavourable condition during a considerable period of time.

(The NERVES of the Stomach and Intestine are described in the article "SYMPATHETIC NERVE.")

(*William Brinton.*)

SYMPATHETIC NERVE.—The term sympathetic nerve is applied to denote a series of ganglia arranged along each side of the spinal column, connected by intermediate bands of nerve fibres, so as to present the form of two gangliated cords. These extend from the upper part of the cervical region to the lower extremity of the sacrum, where the cords of opposite sides are united in a single ganglion or plexus situated in front of the coccyx. The ganglia in each cord correspond in number to the vertebræ, except in the cervical region, where only three ganglia commonly exist. The gangliated cord of either side forms communications with all the corresponding spinal nerves along its course. Branches are also sent upwards from the superior cervical ganglion into the head which communicate with nearly all the cranial nerves, and with which several small ganglia, arranged in different parts of the skull, are connected. From the gangliated cords branches also pass inwards for the supply of the bloodvessels, as well as to almost all the different viscera in the body. These branches are remarkable for their tendency to form plexuses, from which subsidiary branches are sent off to the various viscera in their vicinity. Connected with these plexuses, as well as with the branches which pass off from them, are numerous ganglia of different sizes.

This nerve has been variously named by authors. The older anatomists described it under the name of the great intercostal nerve. From the fact of its being chiefly distributed to the viscera belonging to the circulatory, digestive and generative systems, it was termed by Chaussier the trisplanchnic nerve; and under the supposition that it alone influences the organic processes, it was termed by Bichat the nervous system of organic life. The name sympathetic, or great sympathetic, was given it by Winslow, from its being believed to be the channel through which are effected the different sympathies sometimes found to exist between distant organs when in a morbid condition.

For the sake of description the sympathetic may be regarded as consisting of two portions; the one corresponding to the right and left gangliated cords situated on each side of the vertebral column, the other to the different plexuses occurring on the branches which are sent inwards for the supply of the viscera and bloodvessels. It is commonly further subdivided into a cervical, thoracic, lumbar, and sacral portion. In the following account of its descriptive anatomy it is proposed to describe, 1st, the gangliated cord of the sympathetic, and 2nd the different plexuses formed by its branches in the several regions of the body already specified.

I. *Cervical Portion of the Gangliated Cord.*—The cervical portion of each gangliated cord lies in front of the vertebral column, separated from it by the rectus capitis anticus major and longus colli muscles. It is situated behind the internal and common carotid arteries, the internal jugular vein, and pneumogastric nerve. It presents commonly but three ganglia, named, according to their situation, superior, middle, and inferior.

1. The *superior cervical ganglion* is situated at the upper and lateral part of the neck, in front of the transverse processes of the second and third cervical vertebræ, upon the rectus capitis anticus major muscle, behind and to the inner side of the internal carotid artery and the pneumogastric and glossopharyngeal nerves, with the sheath of which it is more or less intimately connected by some cellular tissue. It is the largest of the ganglia in the sympathetic cord; it varies considerably in its form and size. In general it presents an elongated oval, or spindle-shape, and measures from 4 to 8 lines in length, 2 to 3 in breadth, and about 1½ in thickness. According to Flourens it is generally bifurcated at its lower extremity, and frequently presents a constriction about its middle which appears to divide it into an upper and lower portion. The branches connected with this ganglion are the following:

(*a*) *Communicating branches* pass between it and the three or four upper cervical nerves. They vary in number, and are connected with the posterior aspect of the ganglion. It also forms communications with the pneumogastric, hypoglossal, and glossopharyngeal nerves. The branch of communication with the ninth, or hypoglossal nerve, consisting of one or two delicate filaments, joins it near the base of the skull. This communication is regarded by Sœmmering, Cloquet, Hirzel and others as very rarely existing. In twelve bodies examined by the latter, he found it present only twice. Arnold, Longet and others regard the communication as constant. The communication with the pneumogastric nerve is twofold. One small branch passes between the superior cervical ganglion itself and the ganglion on the trunk of the vagus; another branch, also of small size, passes upwards from the ascending branch of the superior cervical ganglion, and divides at the base of the skull into two filaments, one of which becomes connected with the ganglion of the root of the pneumogastric, while the other terminates in the petrosal ganglion of the glossopharyngeal nerve.

(*b*) *Ascending or Carotid Branch.*—This branch may be regarded as a prolongation upwards of the sympathetic cord. It is soft, and presents a more or less greyish-red aspect. On approaching the inferior orifice of the carotid canal in the temporal bone, it commonly divides into two branches which pass along the canal with the internal carotid artery, the one being situated rather to the inner, the other to the outer side of the vessel; they form numerous intercommunications with each other, giving rise to what is termed the internal carotid plexus.

(*c*) *Pharyngeal Branches.*—These, from three to six in number, leave the upper and inner margin of the ganglion, pass inwards and downwards, and unite with the pharyngeal branches of the glossopharyngeal and vagus nerves to form the pharyngeal plexus.

(*d*) *External lateral Branches.*—These vary in number; sometimes there are only two present; at other times as many as six or eight. They have a greyish-red colour, and from the softness of their texture were termed by Scarpa nervi molles, from their being chiefly distributed to the blood vessels, they were named by Sœmmering vascular branches. They arise from the front of the ganglion, and pass downwards along the internal carotid artery to the point of division of the common carotid, where they give rise to the external carotid plexus. Some filaments also unite with the superior laryngeal nerve.

(*e*) *Superior or long cardiac Nerve*, named also the superficial cardiac branch, varies in thickness, and is sometimes absent. It arises from the anterior and lower portion of the superior cervical ganglion, sometimes from the intermediate cord between that and the middle cervical ganglion, and sometimes it derives filaments from both sources. It runs downwards upon the longus colli muscle and to the inner side of the sympathetic cord, and passes behind or in front of the inferior thyroid artery. In its course through the neck it forms communications with the external laryngeal and descendens noni nerves; it also communicates with the vagus and recurrent laryngeal nerves, and sometimes with the phrenic. Not unfrequently it is joined by the cardiac branches, which leave the middle and inferior cervical ganglion. It passes into the chest in front of or behind the subclavian artery, and along the arteria innominata, to terminate in the cardiac plexus. The nerve of the left side, after entering the chest, runs along the left carotid artery to the arch of the aorta, passing sometimes in front and sometimes behind that vessel.

(*f*) *Communicating cord between the superior and middle cervical Ganglia.*— The connecting cord between the superior and middle cervical ganglia is commonly single, but occasionally consists of two distinct portions. It passes from the inferior extremity of the superior cervical ganglion, which sometimes seems to be prolonged downwards into it, along the surface of the rectus capitis anticus major muscle, behind the carotid artery, and rather to the inner side of the pneumogastric nerve, as far as the inferior thyroid artery. Before sinking into the middle cervical ganglion it sometimes divides into two portions, one of which passes in front, the other behind the vessel just mentioned. The communicating branches with the third, fourth and fifth cervical nerves frequently join it instead of passing to the cervical ganglia. There is also, according to L. F. Meckel, sometimes formed upon it, above the inferior thyroid artery, a small ganglion termed by some the superior thyroid ganglion, and by others the middle cervical ganglion.

2. *Middle cervical ganglion*, smaller than the superior ganglia of the same name, presents an irregularly oval or triangular shape, and is situated on or near the inferior thyroid artery. Communicating branches pass between it and the fifth and sixth cervical nerves; it is also sometimes connected by filaments of communication with the vagus and phrenic nerves. From the inner side of the ganglion several delicate greyish filaments pass off which surround the inferior thyroid artery forming a plexus, which is termed the inferior thyroid plexus. These branches communicate with the recurrent and internal laryngeal nerves, as well as with the upper cardiac nerve. The middle cervical ganglion also gives a branch which is sent to the cardiac plexus. This branch, termed the middle or deep cardiac nerve, arises from the ganglion by from two to four roots which unite into a single or double stem. It passes into the chest in front of the subclavian artery, but sometimes behind that vessel, and runs along the arteria innominata to the deep cardiac plexus. On the left side it enters the chest between the left carotid and subclavian arteries.

3. *Inferior cervical ganglion*, varies in its size and form, which, in general, is more or less semilunar; its convexity being directed downwards, its concave margin upwards. It is situated between the transverse process of the seventh cervical vertebra and the neck of the first rib, behind the subclavian artery, and behind and to the outer side of the root of the vertebral artery. (*a*) Branches of communication pass between the ganglion and the seventh and eighth cervical nerves, as well as the first intercostal nerve. It also sometimes communicates with the phrenic nerve and recurrent laryngæal. (*b*) From the ganglion proceed several fine twigs, which surround the subclavian artery as well as its branches, forming small plexuses about them. One of these accompanies the vertebral arteries; according to some it passes up along with the artery into the cranium, subdividing into as many secondary plexuses as there are branches of the artery. Blandin states that he has followed the branches of the nerve along the basilar artery, upon the posterior cerebral and cerebellar arteries. Whilst situated within the canal in the transverse processes of the cervical vertebra it communicates with several of the cervical nerves. According to M. De Blainville several ganglia occur on this branch, equal in number to the cervical vertebræ, and hence he regards the vertebral branch as the continuation up-

wards of the sympathetic cord. According to Bourgery*, the common sympathetic trunk may be regarded as dividing at the inferior cervical ganglion into an anterior and a posterior portion; the former, corresponding to the continuation of the cord in the neck, he terms the carotid track, the latter, corresponding to the vertebral branch, he terms the posterior or vertebral track. He describes it as arising from the plexus formed around the subclavian artery: it is quite visible to the naked eye at its origin, but higher up its filaments become microscopic in point of size: the vertebral branches, or tracks of opposite sides, unite together in the groove lodging the basilar artery, and communications are also formed between them and the anterior, or carotid track, by means of filaments which pass backwards with the posterior communicating arteries. The vertebro-basilar nervous apparatus, as it is termed by him, supplies nerves to the vessels, which ramify on the cerebellum and posterior lobe of the cerebrum.

(*c*) *Inferior or small Cardiac Nerve.* — The inferior cardiac arises by one or two roots, passes inwards behind the subclavian artery, and terminates in the deep cardiac plexus. It forms communications with the middle cardiac nerve, as also with the cardiac branch of the recurrent laryngeal. Frequently, especially on the left side, the lower cardiac branch becomes united with the middle cardiac, giving rise to what has been termed the Nervus cardiacus crassus. The communicating branch between the lower cervical and first thoracic ganglion is very short, sometimes wanting, the two ganglia running into one another.

II. *Thoracic portion of the Gangliated Cord.* — The thoracic portion of the gangliated cord of the sympathetic lies on each side of the spinal column, in front of the transverse processes of the vertebræ and heads of the ribs, and beneath the pleura. It is continuous above with the cervical portion, and below it passes into the abdomen, between the pillars of the diaphragm and superior extremity of the psoas muscle, outside the splanchnic nerves, becoming continuous with the lumbar portion of the sympathetic cord. The number of the ganglia varies: they are commonly eleven, rarely twelve, on each side. They are, in general, situated between the heads of the ribs in front of the transverse processes of the vertebræ, and present commonly a more or less triangular form. The cord connecting the ganglia of either side runs in front of the heads of the ribs, and is generally single, though sometimes it is double. The branches connected with the thoracic ganglia are the following: —

(*a*) Communicating branches pass between each of the ganglia and the corresponding intercostal nerve: these are commonly double, sometimes three, short, and pretty strong.

(*b*) Branches of small size pass from the ganglia to the descending aorta, forming a plexus around it; others pass to the pulmonary and œsophageal plexuses; branches are also described by Krause as passing between the ganglia of opposite sides in front of the bodies of the vertebræ.

(*c*) The chief branches leaving the thoracic ganglia are the greater and smaller splanchnic nerves. These are situated to the inner side of the main cord of the sympathetic, and also more anteriorly, upon the lateral and anterior surface of the bodies of the vertebræ. They are formed of branches derived from the six lower thoracic ganglia, and pass through the diaphragm into the abdomen. The greater splanchnic nerve derives its roots commonly from the inner part of the sixth, seventh, eighth, and ninth, thoracic ganglia; it often also receives a branch from the fifth, and, according to Dr. Beck, from the different ganglia as high up as the first. It passes obliquely downwards and slightly inwards upon the sides of the vertebral column, in front of the intercostal vessels, and covered by the pleura. It enters the cavity of the abdomen by perforating the pillars between the middle and internal crura of diaphragm, rarely through the aortic opening, and terminates in the semilunar ganglion of the cœliac plexus. The smaller splanchnic nerve, which is sometimes double, springs from the tenth and eleventh thoracic ganglia: following the same course as the greater splanchnic nerve, it is directed obliquely downwards and inwards upon the body of the twelfth dorsal vertebra, passes through the diaphragm between the greater splanchnic nerve and the communicating cord, which unites the last thoracic to the first lumbar ganglion, or pierces the middle crus of the diaphragm. It terminates in the cœliac and renal plexuses; the branch to the latter being generally stronger than that to the former.

(*d*) The communicating cord between the last thoracic ganglion and first lumbar enters the cavity of the abdomen between the middle and external crura of the diaphragm, or penetrates the latter.

III. *Lumbar portion of the Gangliated Cord.* — The lumbar portion of the sympathetic cord generally contains five ganglia, sometimes only three or four, and is situated upon the lateral and anterior aspect of the bodies of the lumbar vertebræ, in front of the psoas muscle, behind and to the left of the aorta on the left side, and behind and to the right of the vena cava on the right. The branches connected with the lumbar ganglia are: — (*a*) Branches of communication with the lumbar nerves: these are commonly two in number for each; they are longer than those in the thoracic region, and pass between the heads of the psoas muscle.—(*b*) Branches also pass off from the ganglia to the aortic, spermatic, renal and superior hypogastric plexuses. — (*c*)

* Mémoire sur l'extremité céphalique du grand sympathetique dans l'homme et les animaux mammifères. Par M. I. M. Bourgery. Comptes Rendus, vol. xx.

Krause describes branches as passing across the bodies of the vertebræ, forming a communication between the ganglia of opposite sides.

IV. *Sacral portion of the Gangliated Cord.* — The sacral portion of the sympathetic cord is situated towards the inner side of the sacral foramina. The ganglia are commonly four in number, are smaller than those in the lumbar region, and decrease in size from above downwards: the cords of opposite sides converge as they pass to the lower extremity of the sacrum, and unite together in front of the coccyx, there being frequently present at their point of union a small ganglion, from which one or two filaments of communication pass to the fifth sacral and coccygeal nerves. The branches connected with the sacral ganglia are communicating branches with the spinal nerves, commonly two in number for each. Several delicate filaments are also sent to the inferior hypogastric plexus.

PLEXUSES OF THE SYMPATHETIC.

A. *In the Head.* — The chief plexuses of the sympathetic which exist in the head are the *internal carotid plexus*, *cavernous*, and *external carotid*. There are also present in different parts of the head several ganglia: the principal of these are the ciliary ganglion, spheno-palatine, otic, and submaxillary. These ganglia have been already described in this work in the articles on the different nerves with whose branches they are connected.

1. *Internal Carotid Plexus.* — The internal carotid plexus is formed by the ascending branches of the superior cervical ganglion, and surrounds the internal carotid artery during its passage through the carotid canal. The ascending branch of the superior cervical ganglion, as was already stated, divides into two portions, one of which passes along the outer and anterior aspect of the artery, while the other lies on the inner and posterior aspect of the same vessel. The external portion is chiefly concerned in the formation of the carotid plexus, the inner in forming the cavernous plexus. The carotid plexus is thus situated chiefly on the outer side of the artery between its second and third bends. The branches connected with the plexus are, —

(*a*) Two or three filaments of communication with the sixth pair of nerves; they join the nerve as it passes along the cavernous sinus. One of these, stronger than the others, was formerly regarded as one of the roots of the sympathetic nerve. One filament is said sometimes to run only a short distance with the sixth nerve, when it leaves it and passes to the ciliary ganglion, or to the spheno-palatine.

(*b*) *Great or deep Petrosal Nerve.* — This branch, commonly termed the deep branch of the Vidian nerve, may be regarded as passing from the fifth pair to the sympathetic, or *vice versâ*. Regarding it as the latter, it may be described as passing out by the superior orifice of the carotid canal, traversing the cartilaginous substance which occupies the anterior lacerated foramen to reach the pterygoid canal, where it becomes associated with the cranial division of the Vidian, along with which it traverses the canal from behind forwards, and terminates in the ganglion of Meckel. In the interior of the pterygoid canal, the two nerves are merely placed side by side with each other, and after leaving the canal are connected separately with the ganglion. The greater or deep petrosal nerve was formerly regarded as the second of the two roots by which the sympathetic was supposed to begin.

(*c*) From three to five delicate short branches pass through the outer wall of the cavernous sinus and join the Gasserian ganglion on its inner surface. One or two of these have been described as passing backwards to the tentorium cerebelli, and have been traced by Arnold to the walls of the transverse sinus. The filaments to the Gasserian ganglion are sometimes supplied by the cavernous plexus.

2. *Cavernous Plexus.* — This name is applied to the plexus formed around the internal carotid artery as it lies in the cavernous sinus; it is situated rather towards the inner surface of the vessel, at the point where it makes its highest turn.

The branches which leave the cavernous plexus are the following: — (*a*) Filaments which join the third nerve; they are two or three in number, and become united with the nerve before its entrance into the orbit. Hirzel regards the communication as rare, having found it only in ten bodies; in some cases he found that the supposed nerve filaments consisted merely of cellular tissue. Bock, Longet, and others regard it as constant. (*b*) Branches of communication to the fourth nerve; they are either derived from the cavernous plexus or from the carotid, and join the nerve as it lies in the cavernous sinus. (*c*) Communicating filaments with the ophthalmic ganglion, one or two in number, emerge from the anterior part of the cavernous plexus, and enter the orbit on the inner side of the ophthalmic division of the fifth nerve, either ending directly in the posterior border of the ophthalmic ganglion, or joining the long root derived from the nasal branch of the ophthalmic. Occasionally one filament enters the posterior border of the ganglion, the other along with the long root derived from the nasal branch. (*d*) One or two delicate filaments have been observed by Fontana, Hirzel, and Arnold to pass from the cavernous plexus to the pituitary body. As this body is said to receive filaments from the sympathetic cords of either side, it has been supposed to hold the same relation to these as the ganglion impar or coccygeal ganglion at the opposite extremity of the trunk. Bock regards the filaments, however, which have been described as entering the pituitary body, as solely destined for its vessels, terminating in their coats. Weber states that he has examined with the greatest care the supposed communication between the sympathetic and pituitary body in mammals and birds, but failed to convince himself that any such communication exists. (*e*) Arterial branches, accompanying the branches of the internal carotid arteries. These are described by Chaussier* and Ribes as passing not only along the anterior and middle cerebral arteries, but also along the branches of the ophthalmic artery, forming minute plexuses upon them. One of these plexuses is described by these authors, as well as by Rusel† and Langenbeck, as accompanying the central artery of the retina into the eyeball. Ribes has also traced filaments from the cavernous plexus upon the anterior communicating arteries, by means of which the sympathetic cords of either side are united, there being at their point of junction a small ganglionic enlargement; this arrangement has been denied by Lobstein and others.

3. *External Carotid Plexus.*—The external carotid plexus formed as already mentioned by the union of the nervi molles from the superior cervical ganglion, commences at the origin of the external carotid artery. There is sometimes a ganglionic enlargement present, which from the fact of being situated at the point of bifurcation of the common carotid artery, was termed by Arnold the intercarotidean ganglion. The external carotid plexus extends along the artery of the same name, encircling it with numerous branches, on which frequently occur small ganglionic enlargements. At its commencement numerous communications are formed between it and the branches of the glosso-pharyngeal and vagus nerves, which go to form the pharyngeal plexus. It also forms connections with the upper cardiac nerve, and, higher up, as it passes with the artery through the parotid gland, branches are given off for the supply of this organ, and also others, which become connected with the facial and auriculo-temporal nerves. Offsets are sent from it along the divisions of the external carotid artery, forming a number of plexuses around them, which are named according to the arterial branches which they accompany. One of these accompanies the superior thyroid artery into the substance of the thyroid gland: it communicates with the superior laryngeal and upper cardiac nerves. Another accompanies the ascending pharyngeal artery, and is intimately connected with the pharyngeal plexus. The lingual plexus encircles the artery of the same name, giving off filaments to the sublingual gland, and forming communications with the lingual branches of the glosso-pharyngeal nerve. The facial plexus surrounds the facial artery and its branches, one or two filaments, which accompany the submental artery, pass to the submaxillary gland, and communicate with the ganglion of the same name. Small plexuses accompanying the occipital and posterior auricular arteries seem to terminate chiefly in the parotid gland. Most of the branches which accompany the superficial temporal artery appear to pass along the arteries going to the ear and eyelids. Numerous filaments, presenting here and there ganglionic enlargements, proceed upwards on the external carotid artery as far as its division into the temporal and internal maxillary arteries; many of these appear to terminate in the parotid gland, while others accompany the temporal and internal maxillary arteries. Of the latter, one is described by Arnold as emanating from the plexus surrounding the middle meningeal artery, and passing to the posterior part of the otic ganglion. Subsidiary branches accompany the different divisions of the internal maxillary artery.

From the external carotid plexus several filaments pass downwards upon the common carotid artery, forming, with others derived from the middle cervical ganglion, a plexus around the vessel, which accompanies it and forms communications with the inferior thyroid plexus, as well as with the superior cardiac nerve and cardiac plexus.

B. *Thoracic Plexuses of the Sympathetic.*—The plexuses occurring in the thorax in connection with the sympathetic are the cardiac plexus, and the plexus surrounding the thoracic aorta: it also contributes to the formation of the pulmonary and œsophageal plexuses.

1. *Cardiac Plexus.*—The cardiac plexus is formed by the union of the cardiac branches of the sympathetic already described, and by numerous filaments derived from the recurrent laryngeal, as well as from the vagus nerve itself; a branch from the descendens noni nerve accompanies the superior cardiac nerve, and also terminates in the plexus. The superior cardiac nerves, the branches from the recurrent laryngeal and vagus nerves terminate in the upper part of the plexus; the middle cardiac branches of both sides terminate commonly in its middle portion, while the inferior cardiac branches, with some of those derived from the recurrent laryngeal nerve, end chiefly in its lower part. The plexus is asymmetrical, and is situated in the upper part of the thoracic cavity, extending from the transverse portion of the arch of the aorta to the base of the heart: it consists of a widely-meshed network of moderately fine filaments, some presenting a greyish, others a more or less white appearance. About the centre of the plexus, behind the arch of the aorta and in front of the bifurcations of the trachea, at the point of division of the pulmonary artery there is commonly present a ganglionic enlargement. This which is termed the cardiac ganglion (Ganglion cardiacum Wrisbergii), presents a greyish colour and irregular shape, generally more or less angular or oblong, and measures from one to two lines in length. That portion of the cardiac plexus which is

* Mémoires de la Société Méd. d'Emulation, vol. vii. p. 97.

† Tiedemann's Zeitschrift. für Physiol. band ii. p. 227.

formed by the branches of the sympathetic which pass down in front of the arteria innominata on the right side, and the arch of the aorta on the left side, corresponds to what is termed by some the superficial cardiac plexus, while the portion formed by the branches of the sympathetic and vagus which descend behind the arch of the aorta between it and the trachea, is termed the deep cardiac plexus. The branches which proceed from the cardiac plexus are the following:—(*a*) Numerous filaments pass off from the upper part of the plexus and surround the arch of the aorta, as well as the large arterial trunks which spring from the same. (*b*) Others pass along the right and left pulmonary arteries, and terminate in the pulmonary plexus. (*c*) Offsets are also sent along the coronary arteries, forming the anterior and posterior coronary plexuses. The anterior coronary plexus is chiefly derived from the superficial portion of the cardiac plexus, and accompanies the anterior or right coronary artery and its divisions; the posterior coronary plexus, chiefly derived from the left side of the deeper portion of the cardiac plexus, is situated at first behind the aorta and pulmonary artery; it then passes in front of the left division of the pulmonary artery to the base of the heart, and reaches the posterior coronary artery, around which it forms an interlacement of filaments. Numerous filaments are distributed by it to the left side of the heart, especially to the left ventricle: the filaments of the anterior coronary plexus are chiefly distributed to the right ventricle. The nerve filaments which leave the coronary plexuses do not all accompany the branches of the coronary arteries, as was formerly supposed; by far the greater number of them run separately from the vessels, and are distributed to the muscular substance of the heart. As regards the arrangement of the nerves on leaving the coronary plexuses, they appear to be much more numerous on the ventricles than the auricles. The filaments distributed to the former are very numerous; they are directed from the base to the apex of the ventricle; those on the anterior surface passing obliquely downwards from left to right, those on the posterior surface from right to left; they thus in general cross obliquely the direction of the muscular fibres of the ventricles, and often also that of the blood vessels. Where they cross the latter, especially in the heart of the young ox, they appear to bifurcate, so as to enclose the vessel in a loop; and at this point there is frequently, as is represented by Dr. Lee, a small enlargement which occasionally contains ganglionic matter.* In their course along the surface of the ventricles, neighbouring filaments frequently unite, there being here also small ganglionic enlargements. According to Dr. Lee there are distinctly visible on the anterior surface of the young heifer's heart about ninety of these ganglia or ganglionic enlargements. The left ventricle appears to be more abundantly supplied with nerves than that of the right side: on the former they can be traced, extending from base to apex, on the surface of the latter they generally extend but a little way down, when they sink into the muscular substance.

2. *Plexus of the Thoracic Aorta.* This consists of delicate filaments which are derived from the thoracic portion of the gangliated chain of the sympathetic; several filaments also pass between it and the œsophageal plexus. Above, it is continued into the cardiac plexus, from which it derives some branches, and below it accompanies the vessel through the aortic opening in the diaphragm, to terminate in the cœliac plexus.

C. *Abdominal Plexuses of the Sympathetic* — The abdominal plexuses of the sympathetic are larger and more numerous than those occurring in any of the other cavities of the body. They correspond in number with the branches of the abdominal aorta, and accompany them in their course to the different viscera. From the plexuses occurring on the larger arteries, off-sets pass, which form a number of subsidiary plexuses upon the smaller vessels. The chief abdominal plexuses are the *cœliac*, *superior mesenteric*, *renal*, *inferior mesenteric*, and *superior* and *inferior hypogastric* plexuses.

1. The *cœliac*, *solar*, or *epigastric plexus* is the largest of the plexuses of the sympathetic. It is situated in the upper part of the cavity of the abdomen, on both sides of the aortic opening in the diaphragm, extending across the anterior part of the aorta, and is covered in front by the stomach. It surrounds the cœliac axis, and extends downwards as far as the origin of the superior mesenteric artery. It usually contains two ganglia; these present a somewhat crescentic form, and have on this account been termed the semilunar ganglia. They are situated one on each side of the plexus towards its upper part, and are commonly surrounded by a number of smaller ganglia. The solar plexus receives the splanchnic nerves, also some branches from the posterior gastric plexus of the pneumogastric; it likewise receives filaments from the plexus which has been described as surrounding the thoracic aorta, as well as others from the three or four upper lumbar ganglia. The offsets from the plexus present the same plexiform arrangement as the plexus itself, and are named according to the arteries which they accompany; they are the phrenic, or diaphragmatic, superior coronary, hepatic, splenic, and renal plexuses.

(*a*) The diaphragmatic plexuses are two in number, a right and left, and consist of several delicate filaments derived from the upper part of the semilunar ganglia. They often present several small ganglionic enlargements, and accompany the diaphragmatic arteries, sinking with them into the muscular

* Dr. Lee, on the Ganglia and Nerves of the Heart. Phil. Trans. 1849.

substance of the diaphragm, where they communicate with branches of the phrenic nerve.

(*b*) The superior coronary plexus accompanies the left coronary artery of the stomach, along its upper border, and is distributed to the anterior and posterior walls of the organ, its filaments uniting with the branches supplied by the pneumogastric nerves, chiefly with those which are distributed to the posterior wall of the stomach. It extends to the pyloric orifice, where it joins branches of the hepatic plexus.

(*c*) The hepatic plexus, of considerable size, ascends along with the hepatic artery; it receives some filaments from the pneumogastric nerve, and also communicates, as has been already mentioned, with the superior coronary plexus of the stomach. Branches leave it for the duodenum and head of the pancreas; and others pass with the right gastro-epiploic artery, along the greater curvature of the stomach, forming the inferior coronary plexus of the stomach. On entering the transverse fissure of the liver, the hepatic plexus divides into a right and a left portion, which accompany the divisions of the hepatic artery and vena portæ, ramifying upon them—an offset from the hepatic plexus passes to the gall-bladder, along with the cystic artery.

(*d*) The splenic plexus surrounds the artery of the same name, passing with it and its branches to the spleen. Offsets pass from the splenic plexus to the pancreas, and to the stomach, which form the pancreatic and left gastro-epiploic plexuses.

2. *The superior mesenteric Plexus* appears as a prolongation downwards of the cœliac plexus, and is the largest of the offsets furnished by it: it also receives some filaments from the right pneumogastric nerve. It surrounds the superior mesenteric artery, forming for it a close plexiform sheath, and sends offsets along its branches, which accompany them as they pass between the layers of the mesentery to the duodenum, small intestine, cœcum, and ascending and transverse colon. The highest of these unite with the nerves which pass along the pancreatico-duodenal artery, while those which are distributed to the transverse colon communicate with the nerves derived from the inferior mesenteric plexus. The nerves which accompany the arteries to the intestines present at first a plexiform arrangement but in their course through the mesentery, several of them are seen to run alongside the vessels, sometimes separated a short distance from them. Communicating branches pass between them in the same way as between the arteries. On reaching the intestine they enter it at the part where the mesentery is attached, and dividing into finer twigs, soon disappear in the substance of its coats. Many appear to become lost in the muscular coats, while some may be traced through these, ending apparently in the mucous coat, or in the sub-mucous cellular tissue.

3. *Renal Plexuses.*—The right and left renal plexuses are formed by branches which proceed from the cœliac and superior mesenteric plexuses, and likewise derive filaments from the aortic plexus. In their course along the renal arteries they receive filaments, which are sent off from the smaller splanchnic nerves, and others from the superior lumbar ganglia. Several small ganglia are present in the nerves of the renal plexus. They divide along with the branches of the renal artery, each arterial branch being generally accompanied by two nervous twigs. From the renal plexus filaments are sent off, which, with others derived from the cœliac and phrenic plexuses, form the supra-renal plexus destined for the supply of the supra-renal capsule.

4. *Spermatic Plexuses.*— The right and left spermatic plexuses consist of some delicate nervous filaments, which are derived from the renal plexus. As they pass downwards with the spermatic arteries, they receive some additional filaments from the aortic plexus, and appear to give off several filaments to the ureters; in their course to the testes they are connected with the nerves which accompany the vas deferens. In the female they are distributed to the ovaries and uterus.

5. *The aortic plexus*, situated along the abdominal aorta, and extending from the superior to the inferior mesenteric arteries, consists of filaments derived from the superior mesenteric and renal plexuses. In its course downwards it also receives branches from the lumbar ganglia: it terminates in the inferior mesenteric and superior hypogastric plexuses, and also, as has been already stated, contributes to the formation of the spermatic plexus.

6. *Inferior Mesenteric Plexus.*—The inferior mesenteric plexus, formed by the left lateral portion of the aortic plexus, is less dense and less distinct than the superior plexus of the same name: its fibres present, however, the same whitish aspect and firm consistence, and sometimes have small ganglionic enlargements developed upon them. It accompanies the inferior mesenteric artery, dividing along with it, and forming secondary plexuses around its branches, which pass with them to the descending colon, sigmoid flexure, and upper half of the rectum. Above, the branches of the inferior mesenteric plexus form communications with those derived from the superior mesenteric, and below, with others derived from the superior hypogastric plexus of the left side.

7. *Hypogastric Plexus.*—The hypogastric, a single plexus, situated in front of the fifth lumbar vertebra and promontory of the sacrum, between the two common iliac arteries, presents an irregularly quadrilateral and flattened aspect. Nervous branches, about twelve in number, pass down to it on each side from the aortic plexus, and additional filaments are derived from the lumbar ganglia. From the plexus small offsets proceed along the common iliac arteries, and a few join the hemorrhoidal filaments derived from the superior mesenteric plexus: it then divides into a right and left

portion, which are continued forwards along the sides of the rectum, to form the inferior hypogastric plexuses.

8. *Inferior Hypogastric Plexuses.* — These consist of a right and left plexus, formed in the manner just mentioned: they contain several small ganglia. Filaments are likewise sent to them from the sacral ganglia, as well as from two or three of the sacral nerves. These plexuses are situated upon the sides of the rectum, the plexuses of opposite sides being united by cross branches. From the plexus proceed the following branches. (*a*) Some hæmorrhoidal branches: these are termed the inferior hæmorrhoidal nerves; they are very delicate and unite with the superior hemorrhoidal branches derived from the inferior mesenteric plexus, and go to supply the rectum. (*b*) Vesical plexus. The nerves proceeding to this plexus come from the lower and anterior portion of the inferior hypogastric plexus, and pass to the sides and lower part of the bladder. The nerves are most numerous near the neck of the organ, and have several minute ganglia developed upon them. From the neck numerous branches pass upwards on the sides of the bladder, and are chiefly distributed to its muscular coats; a few, however, may be traced through the muscular to the mucous coat. From the vesical plexus, filaments are given off which pass to the vesiculæ seminales, around which they form a plexus; others pass to the vas deferens and ramify around it, communicating on the spermatic cord with the nerves of the spermatic plexus, while a third portion passes to the prostate gland. The branches which pass to the latter are of considerable size, and form connections with the plexus around the vesiculæ seminales. Some of the branches sink into the substance of the gland, others are continued forwards to the erectile tissue of the penis, constituting the so-called cavernous nerves, or cavernous plexus. From these branches are distributed to the membranous portion of the urethra. They then continue forwards, passing beneath the arch of the pubis to the root of the penis. By Müller*, they are divided into nervi cavernosi minores, and nervus cavernosus major. The former penetrate the crus of the corpus cavernosus penis, and spread out upon the cells of the erectile tissue: the latter runs along the dorsum of the penis between the dorsal artery and vein. About the middle of the penis it divides into a number of branches and forms communications with the dorsal branch of the pudic nerve: some of the branches accompany the dorsal vessels and unite with those of the opposite side; the greater portion, however, penetrate the corpus cavernosum and are distributed to its substance.

9. *Uterine Plexus.*—The nerves destined for the supply of the uterus are derived from the upper and posterior part of the inferior hypogastric plexus, and also from the superior plexus of the same name. They pass between the folds of the broad ligament in company with the uterine vessels; before reaching the uterus, however, the greater portion of them separate from the vessels, and are distributed to the substance of the neck and body of the organ. The portion derived from the superior hypogastric plexus appears to be chiefly distributed to the fundus of the organ: a filament also passes, according to Dr. Beck*, from the ovarian artery to the fundus of the uterus. Besides the branches above mentioned there are others, according to Dr. Beck, derived also from the hypogastric plexus, which assume a plexiform arrangement around the vessels, and are characterised by the presence of several minute ganglia.

Fig. 280.

Small ganglion from the posterior wall of the cervix of an impregnated uterus of the Cow.

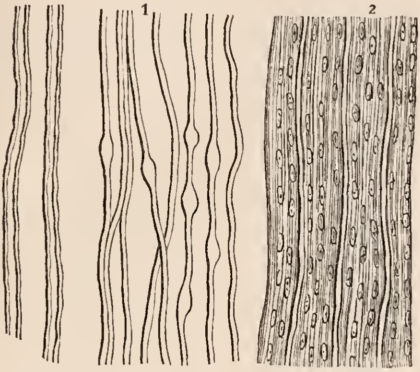
Minute Anatomy. — The branches of the sympathetic nerve present to the naked eye certain characters which, more or less, distinguish them from the proper cerebro-spinal nerves. They have a dull greyish-white appearance, different from the white shining aspect which characterises the nerves belonging to the other class. This appearance is better marked in some parts of the nerve than in others, and is best seen in the branches which accompany the blood-vessels. By Valentin this gray appearance of the sympathetic nerves was attributed to the presence of the ganglionic corpuscles: this, however, as Remak observed, cannot be the case, inas-

* Ueber die organischen Nerven der erectilen männlichen Geschlechts-organe. Berlin, 1836.

* On the Nerves of the Uterus. Phil. Trans. 1846.

much as the ganglionic corpuscles are not distributed throughout the whole extent of the nerve, but are confined to certain limited parts. Remak believed it to be due to the presence of structures termed by him *organic nerve fibres:* Volkmann and Bidder also believed it to be owing to a peculiar set of fibres, different,

Fig. 281.



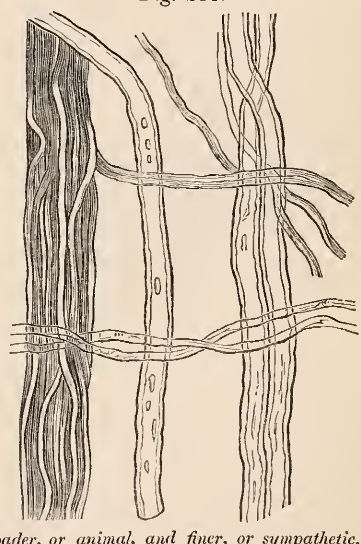
1. *Tubular nerve-fibres from the thoracic portion of the sympathetic cord in Man.*
2. *Fibres of Remak (gelatinous fibres) and fine tubular nerve-fibres, from the nerves of the spleen in the Sheep.*

however, from those of Remak. Whether it be due to the fibres of Remak or not, it seems to be, at least, best marked in those branches of the sympathetic in which these fibres are most abundant. The sympathetic also differs from the cerebro-spinal nerves in consistence as well as in its appearance, being much softer and more readily torn across than the latter. This may be partly due to the want of the strong distinct fibrous sheath possessed by the latter, and partly also to a difference in the character of the nerve fibres themselves. The nerve fibres of the sympathetic are moreover not arranged into distinct fasciculi, but lie together imbedded in a mass of fibrous tissue which accompanies them, serving the purpose of a sheath.

As regards the constituents of the sympathetic nervous trunk, when a portion of one of the main cords is examined with a power of 250 diameters, it is found to be composed of the following elements: 1st. Tubular nerve fibres; 2nd. Structures which present a homogeneous flattened appearance, and contain a number of oval nuclei imbedded in them at intervals; and, 3rd. a quantity of white fibrous tissue.

The tubular nerve fibres which are present in the sympathetic, differ much in point of breadth from one another. Some of them measure about $\frac{1}{2000}$ to $\frac{1}{1600}$ of an inch in diameter: their contents present the arrangement of *double contour* and *axis cylinder* which characterise the fibres occurring in the cerebro-spinal nerves. Besides these fibres there are others present which have also the character of the tubular fibre, but are much finer, measuring only from the $\frac{1}{9600}$ to the $\frac{1}{4500}$ of an inch. They present distinct margins, but have a paler aspect than the above, and do not possess the double contour which is seen in the broader tubular fibres, and many of them often have a tendency to the formation of varicosities. When running in bundles they have, according to Volkmann* and Bidder, who first called attention to their anatomical characters, a yellowish grey hue instead of the white pearly aspect of the cerebro-spinal nerves. Sometimes the two sets of fibres are intermingled and run side by side with each other, at other times they run in bundles more or less distinctly separated. The number of fine fibres which are present much exceeds that of the broader or coarser variety. The two classes of fibres do not, however, appear to be distinctly marked off from one another, there being present fibres which possess partly the characters of the one and partly those of the other. When one of the finer variety is examined at the same time with one of the coarser variety, and the two compared, the points of distinction are sufficiently

Fig. 282.



Broader, or animal, and finer, or sympathetic, primitive nerve-fibres, from the common trunk of the vagus in the Frog. (*Bidder and Volkmann.*)

marked, but a gradual transition from the fibres belonging to the one set to those belonging to the other may, in some parts of the sympathetic, generally be traced. The finer the nerve tubules are, the less distinctly do their contents appear to be separated into central portion or axis cylinder, and white substance of Schwann.

2. In regard to the structures No. 2. which have been mentioned as occurring in the sympathetic, Remak†, their discoverer, describes

* Die Selbständigkeit des sympathischen Nervensystems von F. H. Bidder und A. W. Volkmann, Leipzig; 1842; p. 19. et seq.

† Observationes Microscopicæ, &c. Berol, 1838. §§ 6. 13.

them as being destitute of a sheath, naked, transparent, almost gelatinous, as presenting a number of longitudinal streaks, and as breaking up into delicate fibrils, which in their course present oval dilatations or swellings, and have moreover a number of round or oval corpuscles arranged upon them at intervals. Apparently, the same structures have been described by Henle under the name of "gelatinous fibres." According to him they are flat homogeneous fibres, measuring from the 0·002‴ to the 0·003‴ in diameter, and characterised by the presence of numerous nuclei, some round, others oval, their long diameter being directed in the longitudinal axis of the fibre. They are dissolved by acetic acid, the nucleus becoming at the same time more distinct. The fibres in question are well seen in the branches of the sympathetic which go to the spleen or kidney in the sheep or ox, as well as in the trunk of the sympathetic nerve itself. In the former situations they appear as a more or less transparent, slightly granular, pale mass, and marked by indistinct longitudinal lines into fibres presenting a diameter of about $\frac{1}{7000}$th to $\frac{1}{4000}$th of an inch, and characterised by the presence of round, oval, or elongated nuclei. On the addition of acetic acid they swell out, becoming perfectly transparent and indistinct, while at the same time the nuclei are brought more clearly into view. When treated with tartaric or citric acid, the effect produced upon them is much the same: solution of soda also causes them to swell out and become indistinct, the nuclei being at the same time also rendered more or less indistinct. The nuclei generally measure about the $\frac{1}{4000}$th to the $\frac{1}{2000}$th of an inch in length, and about $\frac{1}{6000}$th to the $\frac{1}{4000}$th of an inch in breadth, presenting the same characters and behaving towards reagents in the same manner as the nuclei occurring in most other tissues. They are much softer than the tubular fibres, and are not easily separated from one another. In some parts of the peripheral branches of the sympathetic these fibres present a much smaller diameter, measuring about $\frac{1}{9000}$th of an inch, are finer and distinguished with difficulty from the white fibrous tissue present. In the nerve they are placed parallel to one another, and are seen, when the preparation is pressed between the glasses, running along each side of the tubular fibres, which latter seem to be imbedded amongst them. They differ from the tubular nerve-fibres in their flattened appearance, want of distinct margin, and in the effects produced upon them by reagents, but are especially characterised by the presence of their nuclei. They are most abundant in the more grey-looking branches of the sympathetic, and seem to be the cause to which this appearance is chiefly owing. Sometimes when one of the smaller filaments of the sympathetic is examined, it seems to be entirely composed of these fibres, no tubular nerve fibres being at first seen; solution of soda, however, which, as has been stated, renders the gelatinous fibres transparent, brings into view more or fewer fine tubular fibres. There can be no doubt that in many parts of the sympathetic, especially in the branches distributed to the arteries, the fibres of Remak, or gelatinous fibres, make up the greater portion of their constituents, the tubular nerve fibres existing only in comparatively small numbers Sometimes more or less grey and white bundles of fibres may be seen running alongside each other: such an arrangement is not unfrequently seen in the branches of communication between the sympathetic and the spinal nerves. In such cases, while the white chiefly or entirely consists of tubular nerve fibres, the grey contains a large number of gelatinous fibres, and always in addition to these more or fewer fine tubular fibres.

The gelatinous fibres are present in different proportion in different parts of the sympathetic: they appear to be more abundant in the neighbourhood of the ganglia than in other parts and in the larger peripherical branches they also exist in considerable proportion, but in the final distribution of these they either do not exist at all or only in small number. They appear to be more abundant in the sympathetic of the higher animals than in that of the lower vertebrata. In mammals and birds they exist in considerable quantity: in amphibia, according to Kölliker, they are present but only in small proportion. In some fish, as in the common Ray, the sympathetic ganglia and branches contain a very large proportion of structures which agree with the fibres of Remak in some respects, such as in their relation to the ganglionic corpuscles and tubular nerve fibres, as well as by the presence of a number of small oval nuclei; they differ from them, however, in not being so much affected by acetic acid and in being firmer: the number of tubular fibres occurring in the sympathetic is very small compared with the number of these structures.

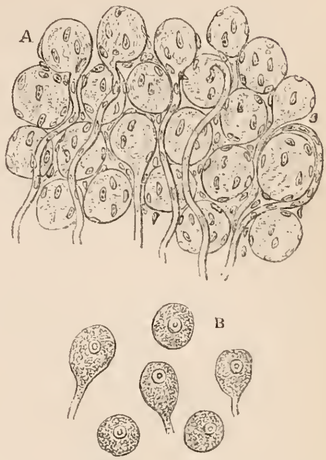
3. The quantity of white fibrous tissue present in the sympathetic trunk and branches is generally considerable; the fibres are arranged in the longitudinal direction for the most part; other fibres, which from their relation to reagents appear to belong to the yellow elastic tissue, encircle the nerve, binding together, as it were, its constituents. After addition of soda or acetic acid the circular fibres are well seen; at the parts where they occur there is frequently observed a distinct constriction, the nerve being swollen out above and below by the reagent applied.

With respect to the nerve fibres occurring in the sympathetic, many of them present undoubtedly the same characters as those occurring in the nerves of the cerebro-spinal system. It has been maintained that the sympathetic also contains fibres which differ in their anatomical characters from the fibres of which the latter class of nerves are composed, and which have been termed organic or vegetative nerve fibres.

Ehrenberg appears to have regarded the fine varicose tubular fibres which are present in the sympathetic, as constituting the peculiar organic nerve fibres. According to Purkinje *, the ganglionic nerve-fibres are much finer than those belonging to the cerebro-spinal system or animal fibres. He describes the latter as containing two substances,—an outer, which runs in the form of a tube through the elementary fibre immediately within its sheath, and an inner, which occupies the hollow interior of the former. The tubular sheaths of the elementary fibres of the ganglionic system contain, on the other hand, no double substance ; their contents are homogeneous, and appear to correspond to the axis cylinder or central portion of the animal nerve-fibres ; their sheaths are much stronger than those of the nerve-fibres of the cerebro-spinal nerves, and resist mechanical influences in a high degree. In the fœtus the animal nerve-fibres cannot, according to Purkinje, be distinguished at a certain stage of their formation from those which are characteristic of the sympathetic in the full-grown animal ; and hence he regarded the latter as a less highly developed stage of the former. Pappenheim also appears to have recognised the fibres described by Purkinje, as constituting the peculiar fibres of the sympathetic system.

According to Remak†, the fibres which have been described above as the gelatinous fibres or fibres of Remak, constitute the peculiar organic or sympathetic nerve-fibre, all the tubular nerve-fibres being considered by him as belonging to the cerebro-spinal system. The fibres in question do not take their origin, according to him, from the cerebro-spinal centres, but arise from the ganglionic corpuscles contained in the different ganglia, and then run along with the tubular fibres sent to the sympathetic by the cerebral and spinal nerves. It has been disputed, however, whether the fibres described by Remak are entitled to the character of nerve-fibres, and are not rather to be regarded in the light of accessory structures which serve as a sheath to the true or tubular nerve-fibres. Valentin ‡, who adopts the latter view, states that the fibres in question do not arise from the ganglionic corpuscles themselves, as was believed by Remak, but are continuous with the nucleated substance which forms the sheath or capsule of these bodies, and are thence prolonged upon the nerve-tubes, and are to be viewed as merely discharging the part of a protecting covering or envelope to the latter. They do not, according to Valentin, present the most distant resemblance to nerve-tubes, which could scarcely be the case were they in reality a mere variety of the same structures : in their microscopic character, on the other hand, they agree in every respect with certain forms of white fibrous tissue, especially at certain stages of its formation ; and they are

Fig. 283.



From the semilunar ganglion of man.

A. Ganglionic corpuscles included within their nucleated capsules.
B. Ditto liberated.

entirely wanting, or occur only in small numbers, in the main cord of the sympathetic, where the fibrous tissue is, as well as in many of the peripherical branches of the same, deficient. In the horse the fibres of Remak, which are present in the nerve-branches passing along the mesentery, were seen by Valentin to cease one or two feet from the point at which the nerves enter the intestine. Bidder * and Volkmann also appear to regard them merely as a variety of areolar tissue, observing that their anatomical characters are so different from the known elements of the nervous system as to exclude them from the character of true nerve-fibres. In the mammalia, according to these authors, the areolar tissue which is interposed between the different organs is very abundant, and in this class of animals the fibres of Remak also abound. In birds, where the quantity of such areolar tissue is smaller, these fibres are not so numerous ; and in the cold-blooded animals, where there is very little interposed areolar tissue, the fibres of Remak either fail altogether, or they exist only in very small numbers. From this it would appear that they regard the fibres of Remak as holding the same relation to the tubular nerve-fibres that the areolar tissue holds to the different organs between which it is interposed. They also agree with Valentin in regard to the very marked resemblance between these fibres and white fibrous tissue at certain stages of its formation, and accordingly adopt the view that they are rather to be regarded as white fibrous tissue which has not reached its full development than true nerve-fibres. They find, moreover, as will be afterwards noticed,

* Müller's Archiv. 1839, p. 203. Valentin's Repertorium, band v. p. 78. See also Bidder and Volkman, op. cit.

† Loc. cit.

‡ Ueber die Scheiden der Ganglienkugeln und deren Fortsetzungen, in Müller's Archiv. 1839. Also Valentin's Repertorium, band iii. p. 76. *et seq.*, and band v. p. 79., &c.

* Op. cit. § 12.

that the increase in point of thickness of the nerves leaving a ganglion over those which pass to it is due, not to the presence of a greater number of the fibres of Remak, as might be expected were these true nerve-fibres arising from the ganglionic corpuscles, but to an increased number of fine tubular fibres.

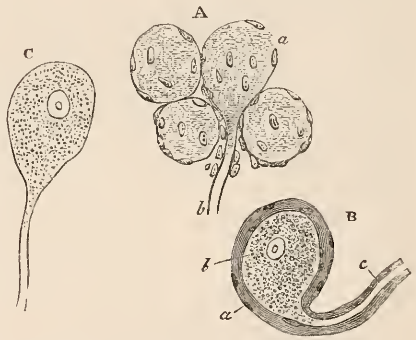
Kölliker * likewise agrees with the authors already mentioned in the view that the fibres of Remak are not to be regarded as true nerve-fibres, but rather as enveloping structures or sheaths to the tubular fibres. He believes, with Valentin, that they are not connected with the ganglionic corpuscle itself, but with its sheath, and are thence continued along such of the tubular fibres as arise from the corpuscles, forming for them a protecting envelope or sheath. The capsules of the ganglionic corpuscles are, according to Kölliker, a species of fibrous tissue; and so also the fibres of Remak, which are continuous with them, must be regarded as partaking of the same nature. Again, whilst, on the one hand, these fibres are very abundant in the neighbourhood of the ganglia, in the finer branches, on the other hand, they are much fewer in number, and in the ultimate distribution of the nerve do not exist at all. Similar structures have also been observed by him accompanying the very fine branches of some of the spinal nerves; such, for example, as those going to the skin, while, at the same time, they are not to be found in the main or larger branches of the same.

The chief grounds, then, on which it is held that the fibres of Remak are to be regarded as enveloping structures, and not as true nerve-fibres, are, 1. the anatomical differences between these and the true or tubular nerve fibre; 2. their resemblance to certain varieties of white fibrous tissue; 3. their connection with the sheaths of the ganglionic corpuscles, and not with these bodies themselves; 4. their absence in the final distribution of the nerve; 5. the increase in the thickness of the nerves *leaving* a ganglion being due, not to an increased number of fibres of Remak, but of fine tubular fibres.

On the other hand, it has been stated that the anatomical difference between the tubular fibres and the fibres of Remak is not a sufficient ground for believing that the latter are destitute of the properties of nerve-fibres. All the nerve-tubes in the embryo, even after it is considerably advanced in development, present much the same character as these fibres, and even after birth nuclei may be occasionally found existing in them. Again, as noticed by Todd and Bowman, the nerve-fibres in the olfactory nerve resemble the fibres of Remak in containing nuclei, and also in the want of double contour, as well as in their soft homogeneous appearance. When a nerve is divided, and a portion of it removed, the structure by which its continuity is restored presents much the same appearance as the fibres of Remak, and this for some time after the part supplied by the nerves has, to a certain extent, regained its functions, showing that impressions may travel along structures not differing from the fibres in question. In reply to the second objection, it is stated that the difference between the fibres of Remak and white fibrous tissue is such as to preclude the notion of the one being a mere variety of the other. In the third place, it is said that it is by no means determined that the fibres of Remak are connected merely with the capsules of the ganglionic corpuscle, and, supposing they were so, that these also may be possessed of the properties of nerve-tissue.

As regards the relation between the ganglionic corpuscles and the fibres of Remak, the tubular nerve-fibres which leave the ganglia may not unfrequently be observed to have structures running along each side, which present the same characters as the fibres of Remak; sometimes only a single row, at other times a double row, of nuclei are placed along each side of the tubular fibre, indicating one or two fibres of Remak. These, on being

Fig. 284.



A. Ganglion corpuscles from one of the spinal ganglia in the Mouse. *a*, corpuscle continuous with a nerve-tube, *b*. (Mag. 250 diam.)

B. Ditto from the Gasserian ganglon of the Cat. *a*, capsule of corpuscle and nerve-tube; *b*, cell-membrane of ganglion-corpuscle.

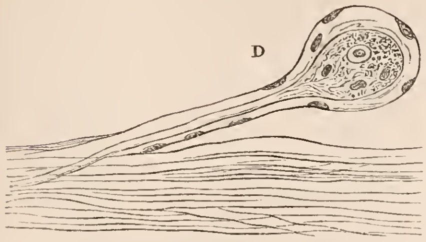
C. Cell freed from capsule.

traced inwards to the ganglionic corpuscle, are found to be distinctly continuous with the capsules of these bodies. When the ganglionic corpuscles are seen separately from one another it is found that these structures are connected only with such of the corpuscles as are still included in their capsules, those which are isolated from their capsules never having any such attached to them (see A, B, and C. *fig.* 284.) In their general aspect, as well as in their relation towards reagents, the fibres of Remak correspond with the capsules of the corpuscles; moreover Kölliker has seen and distinctly figures the capsules of these bodies as directly continuous with the fibres of Remak. As regards their dissimilarity to white fibrous tissue, there can be little doubt that when

* Mikroskopische Anatomie oder Gewebelehre des Menschen, von A. Kölliker; Leipzig, 1850; zweiter band, p. 530.

characteristic specimens of either are examined the difference is sufficiently marked; yet in

Fig. 285.



From a branch of the coccygeal nerve inside the dura mater of Man. (*Mag.* 350 *diam.*) *After Kölliker.*

some parts of the branches of the sympathetic in the higher animals it is difficult to limit the two species of tissue, and between the most characteristic of the fibres and many embryonic tissues the most marked resemblance exists. In the ultimate distribution of the sympathetic there seem to be, as Kölliker observes, none but fine tubular fibres present.

If, then, the fibres of Remak be kept out of consideration, as not being possessed of the properties of nerve-fibres, are there any fibres in the sympathetic which can be regarded as differing in their anatomical constitution from those occurring in the nerves belonging to the cerebro-spinal system? In 1842 Bidder and Volkmann described particularly the distinction in point of structure between the tubular fibres, which have been mentioned as being present in the sympathetic. They measured the tubular fibres, and found that while some of them had a diameter of 0·00046 to 0·00068 of an inch, others measured only 0·00012 to 0·00022; and between the two sizes they observed no fibres of intermediate breadth. They also measured the branches which enter and those which leave the ganglia in the frog. The latter were found to exceed the former in point of thickness, which could only be attributed to the addition of structures arising in the ganglia, and on examination they observed that the increase in thickness of the one over the other was due to the presence of a greater number of tubular nerve-fibres belonging to the finer variety; and hence it was concluded that these are the peculiar organic or sympathetic fibre. The coarser variety they regarded as arising in the cerebro-spinal centres, while the fibres belonging to the finer variety always, according to them, take their origin in the ganglionic system. They describe these fibres as being about half the diameter of those belonging to the cerebro-spinal nerves; they are further distinguished by their paleness; the absence, under all circumstances, of the double contour, and the small quantity of curdlike contents which they present even when examined some time after death, and by their yellowish-gray colour when in bundles. The distinctions between the broad and fine tubular fibres, as given by Volkmann and Bidder, were denied by Valentin, who stated that the fibres of these authors were merely fibres of Remak. Reichert, on the other hand, confirmed the observations of Bidder and Volkmann as to the difference in point of size and structure between the cerebro-spinal nerve-fibres and the sympathetic or organic fibres. The description which is given by Remak of the gelatinous fibre does not, as Volkmann and Bidder maintain, apply to the fibres which they have described: they are much finer, ten times finer, than the cerebro-spinal fibres, whereas the fibres of Bidder and Volkmann are generally only a half narrower than these fibres. The relations of the two structures towards reagents as well as their general characters are also very different.

Kölliker agrees with Bidder and Volkmann that there are nerve fibres in the sympathetic which are not derived from the cerebro-spinal system, but arise from the ganglionic corpuscles; he farther confirms the observation of these authors, that all the fibres which arise in the sympathetic belong to the finer variety of tubular fibres, and that they present the characters which they were described by Bidder and Volkmann as possessing; he denies, however, that they are peculiar to the sympathetic system. Fine fibres agreeing with these in structure arise, according to him, in the cerebro-spinal system, as well as in the sympathetic. Again, the diameter of the coarser and finer varieties of the tubular nerve fibres is by no means so strictly limited as Bidder and Volkmann believed, there being transitions from the finer to the broader or coarser variety. Besides occurring in the sympathetic, they are likewise present in the anterior and posterior roots of the spinal nerves, especially in the latter; and in the brain and spinal cord they exist in large numbers. Another objection to the views of Bidder and Volkmann as to the peculiar nature of these fibres is derived from the fact that it is by no means uncommon for the broader tubular fibres to divide into finer fibres during their course to the periphery, becoming narrower and narrower, and at the same time losing their distinct double contour; and hence in their ultimate distribution they consist almost entirely of fine fibres, which cannot be distinguished from those described by Bidder and Volkmann as constituting the peculiar fibres of the sympathetic system. Volkmann himself now admits that the distinction between the broad or animal nerve-fibre and the fine or organic is by no means always strictly defined, and also that the broad tubular or animal fibres, in their peripherical distribution, assume the characters of the others. It would appear, then, as Kölliker maintains, that there is no absolute distinction between the fibres of the sympathetic and those belonging to the cerebro-spinal system; the difference is merely one of relation and degree: while the nerves of the latter system consist *chiefly* of broad tubular fibres, the sympathetic is *chiefly* composed of fine ones.

Ganglia. — The ganglia occurring on the sympathetic are, as has been already stated, very numerous, constituting the most distinguishing character of this nerve. There are also ganglia present on the posterior roots of all the spinal nerves, as well as on several of the cerebral nerves; and by many these are classified along with those of the sympathetic, constituting what has been termed the ganglionic system of nerves. The ganglia present the appearance of nodules or swellings occurring on a nerve during its course. When examined with the naked eye, they appear to consist of opaque and more or less pellucid portions, present a greyish colour, and are possessed of considerable consistence. Sometimes they occur in the course of a single nerve, as is the case with the ganglia in the posterior roots of the spinal nerves. The sympathetic ganglia commonly present the appearance of masses of various sizes connected with several nerve-branches which appear to pass off from them in different directions. The ganglia situated in different parts of the body are all more or less connected by means of bundles of nerve-fibres passing between them. As already noticed, many of them are arranged alongside the spinal column; others are situated on the different plexuses which are formed by the branches passing off from these, while numerous others of smaller size occur in the substance of the organs supplied by the sympathetic. All of them consist essentially of a number of bodies presenting peculiar characters and termed ganglionic corpuscles, and of nerve-fibres in more or less intimate connection with these.

Ganglionic Corpuscles, ganglion-vesicles (Germ. *Ganglienkugeln*). — These bodies appear to have been first noticed by Ehrenberg*, and were afterwards more fully described by Valentin.† They vary in size from the $\frac{1}{1800}$th to the $\frac{1}{280}$th of an inch. Those in the ganglia of the cerebro-spinal nerves are generally considerably larger and not so delicate as those in the ganglion of the sympathetic. They commonly present a round or oval form; sometimes they are more or less pear-shaped. Their contents consist of a delicate clear fluid holding in suspension numerous finely granular particles, which give the cells a more or less grayish aspect. This substance is possessed of considerable viscidity, as shown by the fact that when removed from the corpuscle it does not separate into distinct particles, but remains coherent in a single mass which flattens out somewhat. Each of the ganglionic corpuscles contains a distinct rounded nucleus which in appearance resembles the corpuscle itself, only its contents are clearer. These measure from the $\frac{1}{3000}$th to the $\frac{1}{1300}$th of an inch in diameter, and are commonly situated rather towards one side of the cell. Within the nucleus there is commonly a third body, which presents a clear rounded appearance like the nucleus, and may be regarded as the nucleolus. Sometimes there are two such bodies present. In the ganglionic corpuscles there is also frequently contained a mass of pigmentary matter consisting of particles which are much coarser and darker than the rest of the contents. This mass is sometimes situated at a little distance from the nucleus, at other times it partly covers it, and occasionally it conceals it entirely from view. Its quantity varies much in different cells: it appears, as Kölliker observes, to be more abundant in the ganglion-corpuscles of old people than in those of the young. Sometimes he has observed it present in such quantity as to fill the entire cell. In the Gasserian ganglion of a man aged about sixty I observed several bodies present, which in size and shape corresponded with the ganglionic vesicles: they appeared, however, to be less delicate, and presented a dark-brown colour, and in all probability were ganglionic corpuscles filled with dark pigmentary matter such as Kölliker notices. Connected with many of the ganglionic corpuscles are one or two delicate processes of different lengths, and presenting the same delicate finely-granular appearance as the vesicle itself of which they appear to be a prolongation. In the corpuscles occurring in the ganglia these do not present the same branching character as they have been described to do in the brain and spinal cord by Purkinje, Remak, Hannover, and by Todd and Bowman, who in their description of these bodies, which by them were termed "caudate nerve-vesicles," hinted at the probability of the processes being continuous with nerve-tubes. The actual continuity of the process of the ganglion-vesicle with the nerve-tube was, however, first observed by Kölliker* in the ganglia of the amphibia. He found that on tracing the process onwards from the cell it became continuous with a nerve-tube presenting distinct dark margins. The observation of Kölliker in regard to the connection of the nerve-tube with the ganglion-corpuscle has since been confirmed by many other observers, and especially by Wagner and others in the ganglia of the fish. Some of the ganglionic corpuscles appear to be destitute of any such process; others have a single process passing off from them, while others present two such processes, passing off at either extremity (A. G. *fig.* 286.). Occasionally the two processes pass off from a round cell, not at either extremity, but at a short distance from each other on one side of the body (*fig.* 291.). The ganglionic corpuscles which are not connected with any process, or, as may be safely said, with any nerve-tube, have been termed by Stannius *apolar* cells; those from which one tube proceeds are termed *unipolar*, while the cells with which two such are connected are called by him *bipolar* ganglionic corpuscles or cells. The nerve-tube which is connected with the unipolar cell is always found to run peripherically, *i. e.* from the centre. In regard to the bipolar

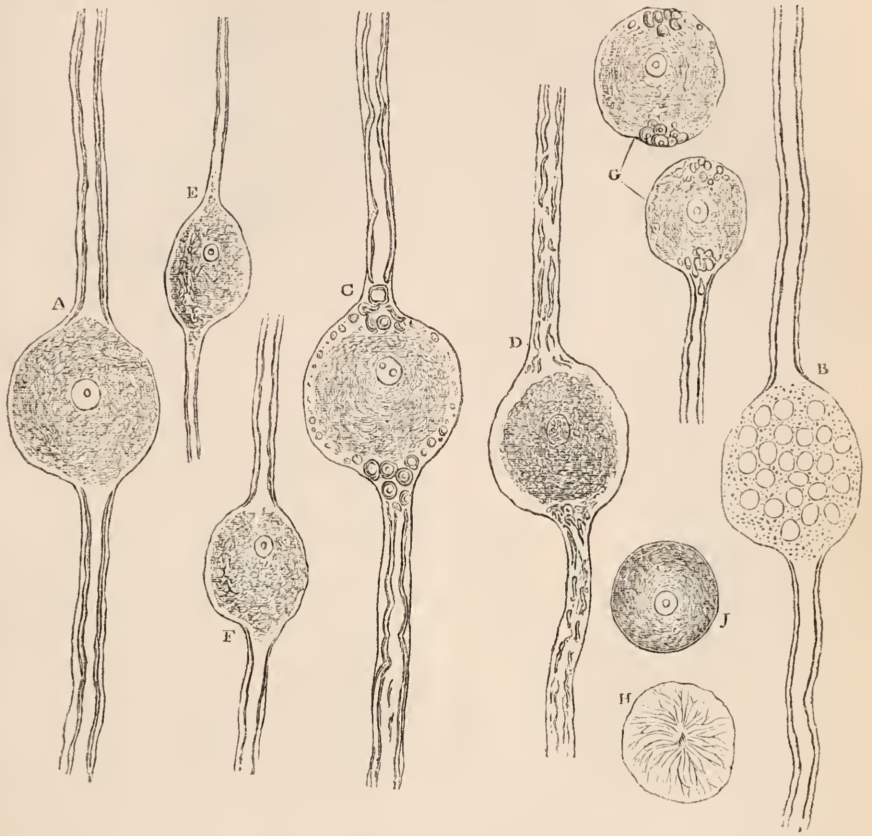
* Poggendorf's Annalen, band xxviii. p. 458., as quoted in Brun's Anatomie.

† Nova Acta, band xviii. p. 127., as quoted in Brun's Anatomie.

* Mikroskopische Anatomie, p. 508., zweiter band.

cells, when the nerve-tubes come off at either extremity, as they generally do, while one of them runs towards the periphery, the one at the opposite runs towards the nervous centres.

Fig. 286.



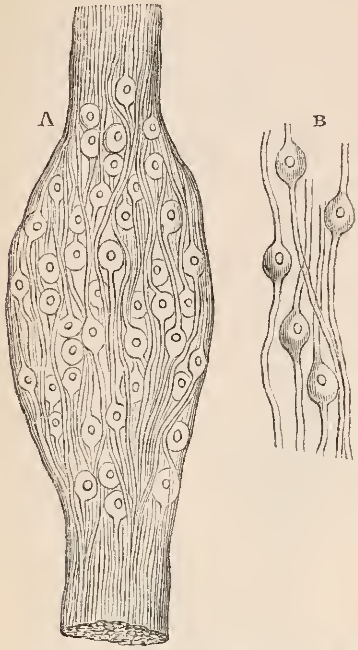
Ganglionic corpuscles from one of the spinal ganglia in the Ray.

In A, the granular contents reach quite to the margin of the vesicle; B, ganglion-corpuscle with a layer of clear round delicate bodies on the inner surface of its wall; C, showing a clear space between the granular contents and the cell-wall, occupied by particles of oily matter similar to the contents of the nerve-tubes; D, a corpuscle which has been treated with chromic acid; E, ganglionic corpuscle of smaller size, with narrower nerve-fibre attached to it; F, one intermediate in size between the larger and smaller corpuscles; G, apparent apolar and unipolar corpuscles; H, collapsed membrane of a ganglion-corpuscle; *j*, liberated contents of the same.

When both nerve-tubes pass off, not at opposite extremities, but from one side of the corpuscle, they both run, according to Bidder, in the direction of the periphery. As regards the mode of connection between the ganglionic corpuscle and nerve-tube, the cell-wall of the former appears to be directly continuous with the membrane of the latter, while the contents of the vesicle seem to be prolonged downwards into the nerve-tube, becoming continuous with its contents. The nucleated substance forming the capsule of the ganglionic corpuscle is also, according to Kölliker, prolonged along the nerve-tube which arises from the corpuscle itself (*fig.* 288. and 289.). All the nerve-tubes which are thus connected with the ganglionic corpuscles in the ganglia of the sympathetic belong to the finer variety of tubular fibres already described. In the spinal ganglia, according to Kölliker, the nerve-tubes arising from the corpuscles are at first fine, measuring about 0·0015—0·0025 of a line; but in their further course many of them increase in diameter up to 0·003—0·004 of a line, or even to 0·005—0·006 of a line, so as to represent broad nerve-fibres, or fibres intermediate between the broader and finer varieties.

Most of the cells which are seen in examining the ganglia of the mammalia belong either to the apolar or bipolar variety. It is possible, however, that many of them, as Wagner, Robin, &c. maintain, although apparently apolar, are really unipolar or bipolar cells, from which one or both processes have broken off during the process of preparing them for examination. That the bipolar cell exists in man and other mammalia, is proved by the observations of Schrœder van der Kolk in

Fig. 287.

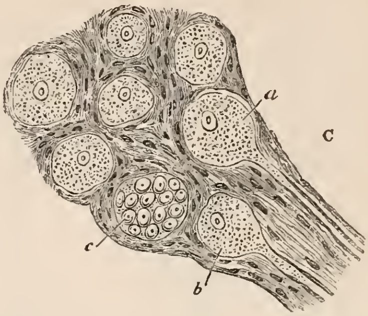


A. Spinal ganglion from the Ray. (40 diam.)
B. Portion of the same more separated.

regard to the cervical ganglia of man, as mentioned by Donders and Harting. Schaffner also describes a bipolar cell in the ganglion Gasseri of the sheep; and similar cells have been observed by Corti* and Pappenheim in the acoustic nerve of the pig, and by Frey in the Gasserian ganglion of the cat. In the common trunk of the pneumogastric and sympathetic nerves in the middle of the neck, in the young calf, oval cells may be seen which have distinctly attached at their peripherical extremity a nerve-fibre; and some of them also appear to be connected with one at the opposite or central extremity.

The different cells composing a ganglion are each surrounded by a more or less clear, homogeneous substance, in which are contained a number of round or oval nuclei. These are seen to form a single or double row around the margin of the ganglionic vesicle, their long axis being directed in the axis of the circumference of the cell (*fig.* 288.). They are also seen upon the surface of the corpuscle (*c*, *fig.* 288.). This substance not unfrequently presents a more or less fibrous aspect, as if composed of spindle-shaped corpuscles. It resembles much (as has been already stated) the fibres of Remak. The nuclei measure from the $\frac{1}{6000}$th to the $\frac{1}{4000}$th of an inch in breadth, and about $\frac{1}{4000}$th to $\frac{1}{1500}$th of an inch in length. The structure in question is closely connected with the walls of the included ganglionic corpuscle, and appears to hold much the same

Fig. 288.



From the gastric ganglion of the Ray, shewing ganglionic corpuscles embedded in a nucleated fibrous tissue.

relation to it that the fibres of Remak hold to the nerve-tubes. It has been termed the capsule of the ganglionic corpuscle. The capsules surrounding the different ganglionic corpuscles are also closely united to each other, so as to form a kind of framework, in the loculi of which the ganglionic corpuscles are placed (*fig.*288.). It would appear also to be prolonged along the nerve-tubes connected with the ganglionic corpuscles for some distance, forming for them an investment or sheath similar to that which it forms for the corpuscles themselves. The quantity of this substance which is present varies in different circumstances. It appears to be more abundant in some cases than in others, and is commonly more so in the sympathetic ganglia than in those on the posterior roots of the spinal nerves.

As regards the arrangement of the nerve-fibres in the ganglia, when one of the entering branches in the ganglia of small animals, such as the mouse, is traced into the point at which it joins the ganglion, it is found to spread out somewhat, and soon breaks up into its component fibres. These separate from one another, running amongst the ganglionic corpuscles, either singly or in bundles of two, three, or more. The nerve-fibres belonging to one bundle leave it and join neighbouring bundles, so that a more or less complete interchange of the fibres contained in the different bundles takes place; and at the same time there is formed a sort of plexus or network, in the meshes of which the ganglionic corpuscles are imbedded (*fig.* 287.). Sometimes, as Valentin observed, one or more of the fibres of one of the entering bundles are seen to wind round the ganglionic corpuscles, and appear again to pass into another entering bundle, thus pursuing apparently a retrograde course. The fibres which thus surround the ganglionic vesicles were termed by Valentin *umspinnende fasern*; whether they again really leave the ganglion in the direction in which they entered it, and in this way may be regarded as terminating in a looped arrange-

* Kölliker's Mikroskopische Anatomie, band ii. p. 519.

ment in the ganglion, it is difficult to determine. Kölliker* has observed that the nerve-tube arising from a ganglionic corpuscle frequently makes one or two turns around it before pursuing its course towards the periphery; and it appears probable therefore that many of the so-called *umspinnende fasern* may be of this description. That the nerve-fibres connected with the ganglia do not merely pass through it between the ganglionic corpuscles, as was formerly supposed, but enter into intimate organic connection with these bodies, either arising from them, or having these bodies developed upon them in their course from the centre towards the periphery, as seems to be the case with most of the bipolar cells, is quite certain.

Aves. — In the bird the ganglia present much the same structure, both as regards the ganglionic corpuscles and nerve-fibres, as those of the mammalia.

Reptilia. — In the frog, the animal in this class which has been most frequently examined, the ganglionic corpuscles present the same general characters as those in the higher animals. The existence of apolar and unipolar ganglionic corpuscles is much better seen in examining the small ganglia in the heart or bladder of this animal than in the ganglia of the mammal or bird. Bipolar cells have been described by Schiff; Valentin† has also described and figured bipolar ganglionic corpuscles the nerve-tubes of which ran in opposite directions, one towards the centre, the other towards the periphery. They were found by him both in the small ganglia of the heart, and also in the ganglia occurring in the main chain of the sympathetic. The nerve-tube connected with these he describes as clear and transparent, differing from the broad nerve-fibres in its colour and general appearance, especially in its not presenting any oily contents, and thus appearing to belong to the fine variety of fibres. Kölliker describes the unipolar ganglionic corpuscles as being pyriform, and at their narrow extremity drawn out into a delicate process. This presents the same pale and finely-granular appearance as the corpuscle itself, and measures from the $\frac{1}{10000}$th to the $\frac{1}{7000}$th of an inch in diameter: after running a short distance from the ganglionic corpuscle it acquires a dark margin and slightly granular contents; becoming, in short, a fine nerve-fibre (see *fig.* 289. A). Bidder has also observed in the ganglia of the heart of the frog bipolar cells, which, however, resembled the unipolar in the fact that both nerve-tubes ran in the direction of the periphery. In the ganglia of the frog there is a much smaller amount of the substance present, which has been described as constituting the capsules of the ganglionic corpuscle, and there are also very few of the fibres of Remak.

Pisces. — In certain animals belonging to this class, especially in the cartilaginous fishes, the connection between the ganglionic corpuscles and the nerve-tubes is much better seen than in any of the preceding classes. In the torpedo and ray the bipolar variety of ganglionic corpuscles was first discovered by Wagner, and shortly afterwards by Robin. Similar observations were also made by Bidder and Reichert, both as regards the cartilaginous fishes, and, by the latter observer, in the cod, perch, and certain species of salmon, as well as in the pike.* In the common ray the ganglionic corpuscles, as occurring in the spinal ganglia, are generally more or less round or oval, and are much larger than in any of the higher animals. They measure from $\frac{1}{400}$th to the $\frac{1}{200}$th of an inch in diameter, and contain a more or less clear viscid fluid with finely molecular matter. On the addition of diluted acids or spirit, they become dark and granular. Each of the cells contains a clear round nucleus, in which there is also present one, sometimes two, nucleoli. The contents of the nucleus, like those of the cell itself, become dark and granular on adding the reagents above mentioned. In several of the cells there are seen, apparently on the inner surface of their wall, a number of round corpuscles, generally clear and transparent, but sometimes more or less dark and granular. They measure about the $\frac{1}{1200}$th of an inch in diameter, and seem, as Wagner and Robin describe, to form a single layer on the inner surface of the ganglionic corpuscles. The larger of the ganglionic corpuscles are generally more or less spherical; the smaller, on the other hand, present commonly a more oval shape. Sometimes between the outer cell-wall and the contents of the vesicles there is, as Bidder describes, a clear space, varying in breadth, generally broadest at the points where the two nerve-tubes are connected with the corpuscle; at other times this space does not appear to exist, the granular contents of the vesicle coming close up to the cell-wall (see A. and D. *fig.* 286.). The wall of the corpuscle appears to be much stronger than that of those in the higher animals, and is distinctly prolonged at either extremity into the membrane of the nerve-tube, the two constituting one continuous structure, agreeing both in anatomical characters and in their relation towards reagents. When the ganglion-vesicle is ruptured, so as to allow its contents to escape, its cell-wall collapses more or less, and often presents the appearance of lines passing outwards towards the circumference, from a central point (H. *fig.* 286.): this appearance is evidently due to folds in the membrane. In the clear space which has been mentioned as sometimes existing between the cell-wall and the contents of the ganglionic corpuscle, there are often observed a number of particles, most abundant at the two poles of the vesicle, which resemble in appearance the curd-like contents of the nerve-

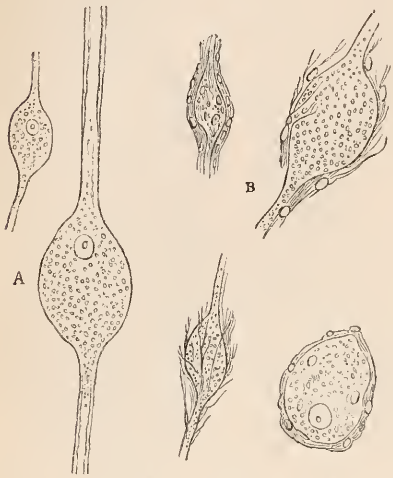
* Mikroskopische Anatomie.

† Valentin, Lehrbuch der Physiologie. Braunschweig, 1848; band ii. p. 602. *et seq.*

* Canslatt's Jahresbericht, 1847, also Wagner's Handwörterbuch der Physiologie, band iii. p. 361. *et seq.*

tubes, and are evidently continuous with the same (C, *fig.* 286.). Sometimes the granular contents of the vesicle appear to be prolonged downwards into the nerve-tube (A. *fig.* 289.),

Fig. 289.



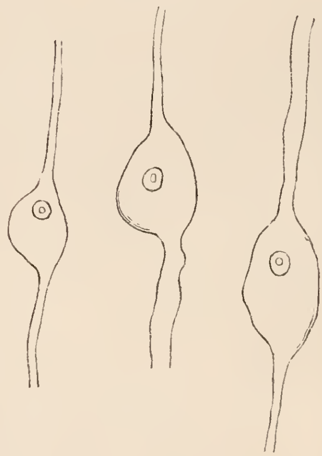
Ganglionic corpuscles from the gastric ganglion of the Torpedo. (After Wagner.)

Showing, B, several of the cells still surrounded by the fibro-nucleated tissue. A, other cells denuded of it.

while at other times, the oily contents of the latter reach quite up to the corpuscle, and seem either to become blended with the granular contents of the same, or are prolonged into the clear space. Wagner* believes that the normal relation between the nerve-tubes and corpuscles is, that each primitive nerve-fibre coming from the centre, retains its appearance of double contour up to the ganglion-cell, where its contents are interrupted by the finely granular matter of the latter; at the peripherical extremity of the cell, the nerve-fibre commences in a quite similar manner. Thus then, according to Wagner, the oily contents of the nerve-tube cease on reaching the ganglionic corpuscle. Bidder†, on the other hand, regards the clear white space between the cell-wall and the granular contents as a thin sheet of nervous matter, which serves as a connecting medium between the contents of the nerve-tube on either side of the ganglionic corpuscle.

As regards the sympathetic ganglia in this animal, they appear in some parts to be almost entirely composed of a fibrous structure and of a quantity of granular matter resembling, as Wagner and Robin observe, the gray granular matter of the nervous centres, and containing a number of bodies of a brownish-yellow granular appearance, which do not disappear on addition of acetic acid. In other parts the ganglia contain corpuscles similar to those already described as occurring in the spinal ganglia, with the exception that they are in general perhaps somewhat smaller. They are imbedded in a fibrous structure, which seems to hold the same relation to them as the nucleated substance forming the capsules of the ganglionic corpuscles in the higher animals. It is difficult to ascertain how far the ganglionic corpuscles in the abdominal ganglia are unipolar or bipolar; according to Wagner, they are the same in this respect as the corpuscles in the spinal ganglia, being all bipolar; one tube entering while another leaves the corpuscle. The nerve-tubes which are connected with them belong both to the broad and fine varieties; in general, the narrower fibres are connected with the smaller corpuscles, the broader fibres with those of larger size (*fig.* 290.).

Fig. 290.



Ganglionic corpuscles from the 26th spinal ganglion of the Torpedo, drawn in outline in order to show the different size of the nerve-tubes. (After Wagner.)

It has been already seen that it is almost certain that all the ganglionic corpuscles occurring in the ganglia on the posterior roots of the spinal nerves, at least in this animal, belong to the bipolar variety; it remains to inquire whether all the nerve-fibres in the posterior root are connected with ganglionic corpuscles. When the ganglion, after addition of dilute solution of soda, is examined with a power of about 30 or 40 diameters, it is observed that while many of the fibres soon disappear among the ganglionic corpuscles, several of them can be traced from the point at which they enter the ganglion almost to its opposite extremity, without being connected with corpuscles; but I have never been able to trace them in this manner quite past the ganglion. Wagner, who counted the nerve-tubes contained in the posterior root of the nerve and also the ganglionic corpuscles, found that the number of each corresponded pretty closely,

* Handwörterbuch der Physiologie, band iii. p. 361. *et seq.*

† Zur Leben von dem Verhältnisz der Ganglien, körper zu den Nervenfasern, Leipzig, as quoted in Canslatt's Jahresbericht, 1847.

so that he believes each of them is connected with one of these bodies.

Invertebrata.—The ganglionic corpuscles in the ganglia of the invertebrata appear to be the same in their essential characters as those of the vertebrate animals. Will* recognises two kinds of ganglion-corpuscles in the lower animals. The one he describes as consisting of a membrane and nucleus, the space between the two being occupied by a clear transparent fluid, which becomes granular on the addition of water; in the other variety there are imbedded in the clear transparent fluid numerous small round cells in which no nucleus is visible. The cells belonging to the former variety have always but one process attached to them which consists of a single tube, presenting no division so far as it can be traced, and thus corresponding to the unipolar variety of corpuscle. In the second kind of corpuscles there are several such processes present; the processes attached to some of these cells all run in one direction; in others they pass off at either extremity and run in opposite directions. In the leech, according to Bruch †, there are also two kinds of ganglion corpuscles. The one variety are round and are apolar; the others are connected with nerve-fibres. The latter are situated towards the lower part of the ganglia, and are more numerous than the former: they are more or less pyriform, their wider extremity being directed outwards; their narrower, terminating in a process, is directed towards the ganglia and the nervous cord. Peripherical ganglia, consisting of from one to six or seven cells, are always found at the points where the branches of the nerves divide. Ganglionic corpuscles were also seen by him in the interior of the nerve-tubes, and corresponding to the view taken by Bidder ‡ of the constitution of the bipolar ganglionic corpuscle. Apolar and unipolar cells have also been described by Hannover and Leydig in several other invertebrate animals.

From the fact that in such animals as the torpedo and ray, where the ganglionic corpuscles are easily isolated from each other, they are all found to belong to the bipolar variety, Wagner, Robin, and Bidder believe that all the ganglionic corpuscles in other animals are also bipolar. Kölliker, on the other hand, while he admits that the bipolar cell is most frequent in the fish, maintains that the opposite is the case as regards the higher animals, most of the corpuscles in them belonging either to the apolar or unipolar varieties; and so far as actual observation goes, the views of Kölliker seem to be perfectly correct, inasmuch as, while apolar and unipolar cells are very frequently seen in these animals, the bipolar variety has been seen very seldom. It is possible, however, that many of these unipolar and apolar cells may, as Wagner and Bidder, &c. hold, be really bipolar cells, one or both nerve-tubes having been broken off during the manipulation required for submitting them to examination. In the spinal ganglia of the ray the cells are very easily isolated from each other, whereas in the abdominal ganglia it is very difficult, owing to the amount of surrounding fibrous structure, to isolate them. Now in the former only bipolar cells are seen, whereas in the latter, most of the cells, when isolated, appear to be unipolar and apolar, although it would appear from the observations of Wagner and others, that they are all bipolar, like those in the spinal ganglia. In the higher animals, especially in the mammalia, the ganglionic corpuscles are isolated from one another with as much difficulty as those in the abdominal ganglia of the skate; and hence the probability that many at least of the unipolar and apolar cells which are seen in them, belong to the bipolar variety in reality. On the other hand that apolar and unipolar ganglion-corpuscles really exist, and that too in considerable numbers, in the ganglia of the higher animals, and also in those of the invertebrata, seems to be shown by numerous observations on the smaller ganglia, where no preparation is required, and where, consequently, the above source of fallacy cannot intervene. In the sympathetic cord of the frog, according to Valentin *, groups of ganglionic vesicles may be observed, without a single nerve-fibre connected with them: Ludwig † has also observed in the auricle of the frog's heart small ganglia in which there were eleven ganglionic corpuscles, and only four or five nerve-tubes; in a nerve passing to the bladder of the frog, and consisting of only two nerve-fibres, Valentin counted as many as seven ganglionic corpuscles, ‖ while another, consisting also of only one or two nerve-fibres, was surrounded by twenty-four ganglionic corpuscles.

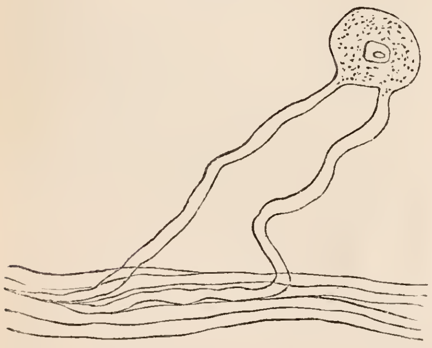
In accordance with the view adopted by Wagner, that all the ganglionic corpuscles are bipolar, the nerve-tube connected with either extremity of the cell running in opposite directions, one towards the centre, the other peripherically, Robin believes that all nerve-tubes arise exclusively from the brain and spinal cord; neither the spinal ganglia nor those of the sympathetic give origin to nerve-tubes; the ganglion-cells are merely organs developed upon the nerve-tubes, between their central and peripherical termination, and several such may be present on a single nerve-fibre during its course. From what has been already stated, however, it seems probable that unipolar as well as bipolar cells exist in the ganglia, and consequently that nerve-tubes do originate in them. That nerve-fibres arise in the ganglia, is further shown by the accurate measurements of Volkmann and Bidder of the nerves passing to and those leaving the ganglia. The ciliary, Gasserian, and spinal ganglia in the frog were found by them to give off a far greater number of fine nerve-

* Müller's Archiv. 1844, p. 76. also in Canslatt's Jahresbericht, 1847.
† Ibid. ‡ Ibid.

* Lehrbuch der Physiologie; Braunschweig, 1848; band ii. p. 602.
† Müller's Archiv. 1848, p. 142.

fibres on the one side than they received on the opposite side. So also in the septum between the auricles of the frog's heart Bidder has seen small ganglia, which gave off on the one side eight nerve-fibres more than they received on the other side. The observations of Bidder and Volkmann have been confirmed also by Kölliker. Engel*, moreover, describes a peripheral ganglion, to which no nerve-fibres passed, while a number of fibres left it; an observation which, if correct, places beyond a doubt the question as to the origin of nerve-fibres in the ganglia. The ganglion in question he describes as being pear-shaped, and about 0·096 of a line in diameter; it occurred in the perichondrium of the tracheal cartilage, and consisted of fourteen ganglionic corpuscles, with seven efferent nerve-fibres, each measuring about 0·0012 of a line in diameter. Even in regard to the bipolar ganglionic corpuscles, it does not appear to be at all certain that they are all merely organs developed on the course of a nerve-fibre arising in the brain and spinal cord. On the contrary, it would appear that several of the cells belonging to this variety must also be regarded as giving origin to nerve-fibres in the same manner as the unipolar cell. Thus Bidder has seen bipolar cells, the nerve-tubes connected with which did not run in opposite directions, one towards the brain and spinal cord, the other towards the periphery, but both ran in the latter direction (*fig.* 291.) : so also Stannius, as mentioned by Kölliker, has

Fig. 291.



Bipolar ganglionic corpuscle, both nerve-fibres connected with which run peripherically. From the spinal ganglion of a Fish. (After Bidder.)

seen in the ciliary ganglion of Trigla, a bipolar cell, both nerve-fibres of which were directed peripherically. The same observer has also seen ganglionic corpuscles in the fish which gave origin to or had three nerve-tubes connected with them.

That most of the bipolar cells are, however, as Robin maintains, organs developed on nerve-fibres of cerebro-spinal origin, in their course towards the periphery, there is no reason to doubt; and moreover that several of these may occur in the course of a single fibre between its central and peripherical termination is also shown by the observations of Stannius on the fish, and by Valentin on the frog. Wagner has also observed two ganglion-corpuscles occurring in the course of a single nerve-fibre, at short distances from one another.

Robin* divides the ganglionic corpuscles into two distinct classes, a larger and a smaller: the larger he finds always occur on broad nerve-fibres, or fibres of animal life, while the smaller are always connected with nerve-fibres belonging to the finer variety, or fibres of organic life; and in this way, according to him, we have a good mark by which to distinguish the animal from the organic nerve-fibres. In the ray, according to Robin, the larger variety of corpuscles measure 0·095 to 0·150 mm. in diameter, are spherical, and often flat at both poles; the smaller measures 0·080 to 0·115 mm. in length, and 0·050 to 0·070 mm. in breadth, and are commonly oval. In the larger cells there is a layer of clear round bodies, without nuclei; in the smaller ganglionic corpuscles the outer membrane is finer, and each of the cells, on their inner surface, is provided with a central dark nucleus. Bidder † also agrees with Robin in separating the ganglionic corpuscles into two groups. In the pike the one set measure 0·042‴, while the other set do not measure more than 0·018‴: the former chiefly occur in the ganglia of the cerebro-spinal nerves, the latter in the ganglia of the sympathetic; the former are always connected with broad fibres, the latter with fibres belonging to the fine variety. The views of Robin and Bidder are opposed by Kölliker, Valentin, and apparently also by Wagner. The latter admits that in general the ganglionic corpuscles are smaller than those occurring in the spinal ganglia, and that the smaller corpuscles have, as Robin observes, an oval shape, while the larger are more or less spherical: there are, however, according to him, cases where broad nerve-fibres are seen passing off from small cells, and where the large cells are connected with small or narrow fibres. Sometimes, indeed, the ganglionic corpuscle has a narrow tube on one side, and a broad one on the opposite side (see *fig.* 290.); and sometimes the broad, sometimes the narrow, runs peripherically. Stannius has, as mentioned by Kölliker, observed in *Petromyzon* cells present, of the fibres connected with which the one was six times broader than the other. Although, however, there does not appear to be a distinct demarcation between the ganglionic corpuscles belonging to the two sizes, there can be little doubt that the cells occurring in the sympathetic ganglia are generally smaller than those occurring on the cerebro-spinal nerves, both in the fish and also in the higher animals. The larger cells in the spinal ganglia of the

* Engel in Zeitschrift der Wien. Aerzte, iv. p. 307., as quoted in Kölliker's Mikroskopische Anatomie, p. 532.

* Annales des Sciences Naturelles, tom. septième, 1847, p. 282.; also Canslatt's Jahresbericht, 1847.

† See Canslatt's Jahresbericht, 1847.

ray appear, as Robin states, to be (in general at least) connected with broad fibres, while the smaller cells are connected with narrow fibres: this, however, does not appear to be invariably the case. In the sympathetic ganglia there are sometimes seen connected with narrow fibres cells as large as some of those in the spinal ganglia, which are connected with broad fibres. Moreover, as already stated, there appear to be transitional sizes between the larger and smaller variety of corpuscles. Kölliker also calls attention to the fact that small ganglionic corpuscles occur in other parts than in the sympathetic, as for example those in the brain and spinal cord. It would seem, then, that just as the finer variety of tubular nerve-fibres cannot be regarded as characteristic of the sympathetic system, so also the smaller variety of ganglionic corpuscles cannot be regarded as peculiar to it either.

It has been already stated, that the nerve-fibres which compose the posterior root of the spinal nerves in the ray, &c., have all, according to Wagner, ganglionic corpuscles developed upon them. He concludes from this, that all sensory fibres are so constituted, and that we have thus a good mark by which a sensory nerve-fibre may be distinguished from one possessed of motor properties. To this view, however, it is objected by Kölliker, that in the higher animals at least, so far is it from being the case, that all the fibres in the posterior roots of the spinal nerves are provided with these structures, that not one of the fibres proceeding from the spinal cord enters the ganglion at all, the nerve fibres connected with the ganglion being fibres which arise in it and run peripherically, not one of them passing in the opposite direction towards the spinal cord. In examining the spinal ganglia of the mouse, after addition, as Kölliker directs, of dilute solution of soda, I have often had no difficulty in observing, that a great portion at least of the fibres in the posterior root run past the ganglion without forming any connection with its corpuscles, and, moreover, that the fibres of the ganglion appear to be directed peripherically, as he states.*

Connection between the Sympathetic and Cerebro-spinal Systems. — By the older ana-

* A paper on multipolar ganglion-cells has been published by Remak in the Monatsbericht der Königl. Preuss. Akademie der Wissenschaften zu Berlin für Januar., 1854, translated also in the Edinburgh Monthly Medical Journal for April, 1854. He mentions that it was first made known by Stilling's discovery of the so-called nerve-nuclei in the pons Varolii of man and of the mammalia, that the multipolar ganglion-cells discovered by Purkinje, Müller, and himself (1837), in the central organs of the vertebrata are connected with motor nerve-fibres. It has also been ascertained by Wagner (1847), that each of the large multipolar ganglion-cells of the electric lobes in the torpedo becomes continuous by means of a process with the axis cylinder of a fibre of the electric roots of the n. vagus and trigeminus. The other branched processes of these cells, distinguished by their granular or striated appearance, serve the purpose, according to Wagner, of connecting the cells with each other. Remak could not, however, in an examination of the Torpedo marmorata find such connections. On treating the fresh brain with a solution of sublimate or of double chromate of potash, the electric lobes are easily separated into their constituents. All the ganglion-cells are multipolar, surrounded by delicate nucleate sheaths, and occupy the meshes of a network formed of wide vessels with thick walls. The processes destined for the formation of the electric roots of the vagus and trigeminus collect themselves at the base of the cerebral lobes into strong bundles visible to the naked eye. The remaining branched processes, becoming surrounded by a thin medullary sheath, form nerve-tubes with dark borders, which pass into the medulla oblongata. A connection of the cells with sensory fibres has not as yet been demonstrated; the sensory roots of the vagus and trigeminus do not pass into the electric lobes; rather those of the former pass into the medulla oblongata, those of the latter into a gray appendix of the cerebellum (feuillet restiforme of Lerres and Lavi), which in its structure, particularly in the size and form of its multipolar ganglion-cells, agrees with the cerebellum, but not with the electric lobes.

He mentions that he has in his possession transverse and longitudinal sections from the spinal cords of man and of the ox, prepared by Stilling, in which, as mentioned by the latter, the passage of nerve-fibres belonging to the motory roots into multipolar ganglion-cells of the anterior gray column is observed. He finds also in the transverse sections small bands of broad nerve-fibres with dark borders, which seem to unite the anterior and posterior roots. From the place of entrance of the anterior roots into the anterior gray columns, or commencing at the outer circumference of the latter, they run as far as the posterior surface of the substantia gelatinosa, where the posterior roots enter the latter. Here they are connected with the ganglion-cells, which send one of their processes to the sensory roots, while the chief mass of the latter radiates in broad thick bands through the gelatinous substance into the posterior gray columns as far as the seat of the large multipolar ganglion-cells. These circular bands of fibres may be presumed to indicate one of the paths on which in decapitated animals the stimuli applied to sensory nerves gives rise to reflex movements. It is remarkable in this respect, that the long axis of the largest ganglion-cells has the same direction as the long axis of the spinal cord, and that besides the lateral processes by whose means they are connected with the fibres of the roots of the nerves, they send out branched processes at both poles towards the cephalic and caudal extremities of the spinal cord.

In the spinal ganglia the multipolar cells discovered by Remak in 1837 in the ganglia are not found. They consist rather, as he observed, in fresh plagiostomes, without exception of the bipolar cells simultaneously described by Robin and Wagner (1846). These constitute, as shown by Leydig in Chimæra monstrosa, nucleated swellings of the axis cylinder, and are surrounded by a sheath consisting of an epithelial layer, and of a firm membrane, which is continuous with the sheath of the nerve-tube. Bipolar cells may also be obtained from the spinal ganglia of man and of the mammalia. They frequently appear unipolar when the two processes leave the cell close to one another. More frequently, however, as Kölliker observes, are cells seen with a single process; this probably divides after a short course into two fibres. He finds at least in the spinal ganglia of the mammalia (ox), not unfrequently, divisions of nerve-tubes with dark borders, which he misses in the plagiostomes.

Of the ganglia, it is exclusively the sympathetic which are made up of multipolar ganglion-cells. The sheath of the latter consists, as in the spinal ganglia, of a delicate layer of cells and of a strong tomists, the sympathetic was described as a continuation of the fifth and sixth cranial nerves, reinforced by fibres sent to it from the different-cerebro spinal nerves along its

membrane. The number of processes varies between three and twelve; by speedily branching they may be increased threefold and upwards. The number is regulated by the number of nerves connected with the ganglion; and hence it is smaller in the main cord than in the solar plexus. The processes have in general the optical and chemical properties of the axis cylinder of the nerve-fibres. In the solar plexus there are found, however, ganglion cells whose processes are distinguished from one another in a similar manner to those of the ganglion cells in the electric lobes of the torpedo. Besides the multipolar ganglion cells, bipolar cells are also observed in the plagiostomata and mammalia. They differ from those of the spinal ganglia, however, in this, that both processes branch, thus coming to agree essentially with the multipolar cells. The same holds of the unipolar cells which, in the animals mentioned, are sometimes found along with multipolar, and which in the batrachia and osseous fishes, as well as in the head of the mammalia, almost alone constitute the sympathetic ganglia. In transverse or longitudinal sections of the thoracic or abdominal sympathetic ganglia in the mammal or plagiostome, the simple (generally very broad) processes of such a unipolar cell are seen after a short course to divide into numerous fibres, which pass off from one another in different directions. That all the processes take a peripherical course cannot, according to Remak, be demonstrated, and is, from what follows, improbable.

He has ascertained, namely, that in the mammalia the multipolar ganglion-cells of the ganglia in the main cord of the sympathetic in the abdomen and thorax become continuous by means of their processes with the axis cylinder of nerve-fibres with dark borders, of such, too, as pass from the spinal ganglia into the ganglia of the main cord. In man and in the mammal, each ganglion in the main cord is connected, by at least two branches, with spinal nerves. The under branch (ramus communicans sympathicus s. revehens) is, according to his observations, gray, contains very fine (the fibres of Bidder and Volkmann) nerve-fibres, and very many ganglion-fibres: it joins a spinal nerve for peripherical distribution after it has at its place of entrance, sometimes close to the spinal ganglion, formed another ganglion consisting of multipolar cells. The upper branch (ramus communicans spinalis, s. advehens) is white: it contains the fibres which, according to Wützer, &c., may be followed to both roots of the spinal nerves. Remak has as yet succeeded in seeing fibres of this branch enter merely into the anterior root; the remainder, generally the smaller number, are lost in the spinal ganglion. The sensory fibres destined for the sympathetic nerve must, therefore, as it appears, become connected with cells of the spinal ganglia before they pass into the main cord of the sympathetic. The fibres of this spinal communicating branch either pass directly into the ganglia of the main cord, or they form in part separate white bundles, which apply themselves to the cord, and are lost in the next ganglion behind. Since, now, as transverse sections of the glangia in the main cord show, all entering spinal fibres become connected one after another with multipolar glanglion-cells, it follows that if the anterior roots of the spinal nerves contain merely motor fibres, the posterior merely sensory, the multipolar cells in the ganglia of the main cord are found as well in the course of sensory as of motory nerve-fibres. From these cells there pass off in the peripherical direction both broad nerve-fibres with dark borders, and fine fibres (fibres of Bidder and Volkmann), likewise others in which no dark borders can be observed. All these peripherical fibres may be named sympathetic, in opposition to the spinal fibres with which they are connected by means of the multipolar ganglion-cells. There are no grounds for the assumption that (human) sympathetic fibres exist which do not stand in connection with spinal fibres, and consequently not in connection with the great central organs of the nervous system. So also in the nerves passing off from the sympathetic ganglia to organs no spinal fibres have as yet been demonstrated in whose course no sympathetic ganglion-cells are found.

By the above results, it is merely established that in the sympathetic ganglia the angles of branching, or points where sensory and motor fibres divide, contain ganglion-cells. The ganglia are not, however, thereby established to have the function of central organs, so far as we make them dependant on the conflux of sensory and motor fibres, and so long as there is no ground for supposing that among the peripherical fibres passing from a sensory or motor sympathetic ganglion-cell, as well sensory as motor fibres are found. Ganglion-cells have been observed by Leydig in the angles of branching of sensory fibres in Carinaria Mediterranea.

In the angles of branching of motor fibres ganglion-cells are only known in the great central organs. This of itself gives ground for the question, whether the sympathetic ganglia have the function of central organs; that is, whether in them there are distinct sensory and distinct motor cells, or whether each multipolar cell serves as a medium of connection between sensory and motor fibres. On the spinal communicating branches, the question has not hitherto been determined, because they are too long, and a trustworthy microscopic distinction between the two kinds of fibres is wanting. On the other hand, other observations favour the view that the multipolar cells are connected both with motor and sensory fibres. In ganglion-cells whose long axis is the same as the long axis of the ganglion, there are frequently seen two fibres entering at one pole and two passing off from the other. If all four fibres were of the same kind, the cell would then form an anastomosis between fibres of the same kind, as has only once hitherto been observed by Leydig, as a variety of the bipolar cells in the Casserian ganglion of Chimæra monstrosa. If, moreover, in a small multipolar ganglion taken from the solar plexus of a mammal (ox), the number and direction of the nerves passing to and from it be compared with the number and the direction of the processes of the cells, as seen on a transverse or longitudinal section of the ganglion, the fullest correspondence is found to exist between them; that is, in such a multipolar ganglion each ganglion-cell is connected with nerve-fibres of all the nerves which are connected with the ganglion. That in these cases, each of the nerves entering or leaving the ganglion contains only sensory or only motor fibres is, however, improbable for this reason, that in other multipolar sympathetic ganglia, — for example, the ciliary, otic, and spheno-palatine,—we know that the entering nerves contain sensory as well as motor fibres.

If the sympathetic ganglion-cells serve as connecting media between sensory and motor fibres, then the impressions made upon sympathetic sensory fibres may be transferred by these ganglion-cells to sympathetic motory; through the medium of the spinal sensory communicating fibres they will also be enabled to act upon the great central organs (brain and spinal cord), and thence through the spinal motory upon the sympathetic ganglion-cells and their motor processes. Besides the sympathetic sensory and sympathetic motory fibres, the assumption of a third set of sympathetic fibres, serving immediately for nutrition, is not required by any fact in physiology, since it is possible to explain the dependence of nutrition upon the nerves by the action of the latter upon the contractile walls of the blood-vessels.

course. The communicating branch between the carotid plexus and the sixth nerve, and the deep or carotid branch of the vidian, were regarded as the roots by which the nerve commenced, while the different branches passing between it and the other cerebral and spinal nerves, were believed also to be entirely composed of fibres sent by the latter to the sympathetic.

According to Bichat, the sympathetic is an independent system of nerves ; the cords which pass between it and the cerebral and spinal nerves are not entirely composed of fibres sent to the sympathetic, but are partly branches transmitted by it to these nerves.

The observations of Petit and Fontana* had already shown that the communication between the sixth nerve and the sympathetic did not consist of fibres sent by the former to the latter, inasmuch as the sixth nerve was found to be thicker beyond the point of junction with the filament than before.

In 1827 Retzius† showed that in the trifacial nerve in the horse there was present a gray fasciculus of fibres distinct from the white, and which seemed to take its origin in the ganglion. Somewhat similar observations were made by Varrentrap and Müller on the branches of the trigeminus, and by Giltay on the glosso-pharyngeal, vagus, and superior spinal nerves of the fish, &c. It was afterwards noticed by Remak that the gray portions of the communicating branches consisted of fibres which were sent by the sympathetic to the cerebro-spinal nerves to be distributed peripherically with them. On microscopic examination it was found by him that the sympathetic contained a large number of fibres presenting a peculiar structure : these he regarded as the proper organic or sympathetic nerve fibres, and believed that while the sympathetic derived from the brain and spinal cord all the tubular fibres contained in it, the grayer portions of the *rami communicantes* were composed of organic or sympathetic fibres, which were sent by the sympathetic to the cerebro-spinal nerves, to be distributed peripherically with them. The same view was also adopted by Müller and others. Valentin, as has been already stated, rejecting the fibres of Remak as being destitute of the properties of nerve-fibres, believed that the *rami communicantes* consisted entirely of fibres sent by the brain and spinal cord to the sympathetic. Volkmann and Bidder, though agreeing with Valentin in regard to the fibres of Remak, still maintained the opinion, that the *rami communicantes* are of a compound nature, containing fibres which are sent to the sympathetic from the cerebro-spinal nerves, and also others which are sent to the latter by the sympathetic, and which belong to the fine variety of tubular fibres already described as probably arising in part from the ganglionic corpuscles.

On examining the connection between the sympathetic and cerebro-spinal nerves in the frog, they find that all the anterior branches of the spinal nerves communicate with the sympathetic. The filament of communication with the first spinal nerve at its entrance into it divides into two portions, one of which proceeds towards the spinal cord, the other towards the periphery : when it consisted of two portions, the one was directed towards the centre, the other ran peripherically. Connected with the second spinal nerve they found several communicating filaments, the smaller portion of the fibres of which ran towards the centre, while the larger portion was directed towards the periphery. The fibres connected with the third nerve also ran in both directions, the chief portion, however, towards the centre. The fourth communicating branch sent its fibres both towards the centre, and also towards the periphery, the portion running centrally, however, being much more considerable than that running towards the periphery. So also in regard to the fifth ; the portion, however, directed towards the centre did not exceed that passing peripherically so much as in the former. Sometimes they found that the central and peripherical portions were about equal. The sixth communicating branch sent about an equal portion of its fibres in either direction. In regard to the seventh, they found that by far the greater portion was directed peripherically, while only a very small bundle took the direction of the centre. Between the eighth nerve and the sympathetic there are frequently two communicating filaments : their fibres are directed almost exclusively towards the periphery, only a very small portion being directed towards the centre ; and sometimes even this is wanting. Between the ninth nerve and sympathetic there are commonly two, often also three, filaments of communication with the sympathetic ; and in one case they found as many as six : the course of the fibres here is similar to what it is in the eighth ; perhaps, however, the portion sent inwards towards the centre is even smaller, and not unfrequently fails altogether. The communication with the tenth nerve they found was not constant : sometimes three communicating filaments were observed ; at others no communication appeared to exist. When present, they always ran almost exclusively in the direction of the periphery. Thus, then, of the rami communicantes in the frog there appear to be none which consist of fibres entirely derived from the spinal cord, while, on the other hand, some of these consist almost exclusively of fibres which run towards the periphery, and which therefore must be regarded as exclusively consisting of fibres which are sent by the sympathetic to the spinal nerves. The five upper spinal nerves give to the sympathetic in the frog more fibres than they receive from it, while, on the contrary, the five lower receive from the sympathetic more fibres than they send to it. As regards the communicating

* Selbständigheit des Sympathischen Nervensystems von Bidder und Volkmann, p. 29.

† Ibid. ‡ Ibid.

branches between the sympathetic and cerebral nerves, they also regard it as probable that the greater number of the fibres in the communicating branches run peripherically. In the fish and bird they also found that the fibres of the communicating branches were directed partly towards the centre and partly towards the periphery. In small animals belonging to the class mammalia, such as the rat and mole, as well as in small dogs and cats, they found, on examining the communicating branches with the microscope as before, that the fibres passed both inwards towards the centre, and also outwards towards the periphery, and that the latter in many cases exceeded the former.

As already mentioned, there are commonly two branches of communication between each of the spinal nerves and the sympathetic in the higher animals. The one of these presents a white appearance, resembling more or less the ordinary nerves of the cerebro-spinal system; the other has frequently a more gray aspect, approaching in this respect the appearance of the sympathetic nerves. Sometimes the white cord presents the appearance of being composed of a white and a grayer portion running together. As regards the minute structure of the rami communicantes, the whiter portion consists entirely of tubular nerve-fibres, both of the coarser and finer varieties ; there are also not unfrequently present fibres which appears to be intermediate in point of breadth. In general the broader variety of fibres appear to be more numerous than those which belong to the finer variety. According to Kölliker, the relation between them is much the same in point of number as in the posterior roots of the spinal nerves. The gray portion, as is stated by Todd and Bowman, contains a large proportion of fibres belonging to the gelatinous variety : in young animals it is often entirely composed of structures agreeing in character with the gelatinous fibre. In the full-grown animal also it often, when examined without addition of reagents, presents the appearance of being altogether composed of these fibres. Addition of dilute solution of soda, however, always brings into view a number of tubular nerve-fibres, which belong to the finer variety. The relation between the tubular fibres and those of the gelatinous kind as regards number, is much the same as in many of the branches of the sympathetic, especially in the smaller twigs distributed to the blood-vessels. Occasionally, however, especially in the rabbit and cat, this portion is found to be almost exclusively composed of fine tubular nerve-fibres : the gelatinous fibres being present only in small numbers. In its appearance as seen by the naked eye, as well as in its microscopic structure, the grey portion of the rami communicantes agrees in character with the branches of the sympathetic, and would appear to be an offset from the same to the cerebro-spinal nerves. This is rendered more probable by the observation of Dr. Beck, that the grey portions on leaving the ganglia send off small branches to the neighbouring vessels, and are reduced in size before reaching the spinal nerves. Moreover, Kölliker has sometimes observed a small ganglion present upon them, which, on examination, was found to present the structure of the sympathetic ganglia, and which gave origin to the fibres with which it was connected.

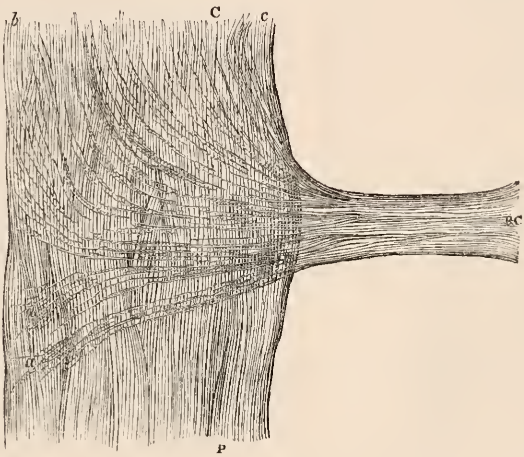
Fig. 292.

From a gray communicating filament between the sympathetic, and one of the lumbar nerves in the Cat, treated with acetic acid, showing fine nerve-fibres, and nucleated fibres of Remak. (*Mag.* 250 *diam.*)

As regards the white portion of the rami communicantes, there can be no doubt that all the broad tubular fibres contained in it are fibres which are transmitted from the nerves of the cerebro-spinal system. This is proved by the fact that all the tubular fibres which are supposed to originate in the ganglia do not belong to the broader, but to the finer variety. In regard to the finer variety of tubular nerve-fibres occurring in this portion, inasmuch as similar fibres are present both in the anterior and posterior roots of the spinal nerves, they may be regarded either as fibres sent from the spinal cord to the sympathetic, or they may be fibres which are transmitted from the latter to the cerebro-spinal nerves. On tracing the white portion of the *rami communicantes* backwards to the spinal nerve, it is found to apply itself to the latter generally in a direction more or less central. On attempting to separate the two by means of needles, though several of the fibres break across, yet the direction of these, as well as of the others, appears to be towards the centre. When the corresponding spinal nerve, along with its communicating branch, is dissected out, and examined, after addition of dilute solution of soda, with a power of 40 diameters, it is not difficult to observe, in the cat or other small animals, that the fibres composing the white portion run towards the centre. Many of them bend directly inwards to the cord, while others sink into the spinal nerve, more or less obliquely, still, however, in the direction of the centre. That the fibres in question are not to be regarded as fibres sent from the sympathetic to the cerebro-spinal nerves is rendered further probable by the fact that they can all be traced beyond the corresponding sympathetic ganglion into the cord above and below. Moreover Kölliker has traced them not only past the ganglia in the main chain of the sympathetic, but into the peripherical branches, and, in small animals, even through the ganglia occurring upon these latter He also finds that the fine fibres in question differ from those which arise in the sympathetic ganglia in presenting a darker contour and in being somewhat broader.

As regards the proportion between the fibres in the communicating branches which may be regarded as proceeding from the sympathetic to the cerebro-spinal nerves and those which are sent by the latter to the sympathetic, we have already seen that in the frog, according to the observations of Bidder and Volkmann, the former exceed the latter considerably. In the higher animals it would appear that the reverse is the case; in the rabbit, according to Kölliker, by far the greater portion of the *rami communicantes* run towards the centre. In man also, according

Fig. 293.



Connection between the sympathetic and the sixth intercostal nerve in the Rabbit.

R C, communicating branch; C P, intercostal nerve; C, its central extremity; P, its peripheral extremity. Most of the fibres of the communicating branch run towards the centre; several of these, *a*, *a*, disappear among the fibres of the intercostal nerve, rather in the direction of the periphery. (Mag. 60 diam.)

to the same observer, much the greater number of the fibres contained in these branches run inwards towards the spinal column. I examined most of the rami communicantes in a fœtal calf about 2½ feet in length, and have little hesitation in saying that in this animal the proportion of fibres which are directed towards the spinal cord greatly exceeds any that appear to run towards the periphery. At the point of junction with the spinal nerve the communicating branch, when examined with a power of 40 diameters, was seen to spread out somewhat, most of the fibres bent directly inwards towards the spinal cord, others passed into the nerve, either obliquely or at right angles to it, and then curved inwards towards the spinal cord. In some of the communicating branches, a few of the fibres were seen to join the nerve in the direction of the periphery. In the cat also, the fibres of many of the communicating branches were found to run exclusively in the direction of the spinal cord.

The fibres in the different communicating branches, as shown by Wützer, Müller, and others, are connected both with the anterior and posterior roots of the spinal nerves, and it seems probable that the fibres which are sent from the cerebro-spinal system are derived from both. Volkmann*, however, as will be afterwards noticed, believes that all the fibres sent to the sympathetic are derived from the posterior root alone.

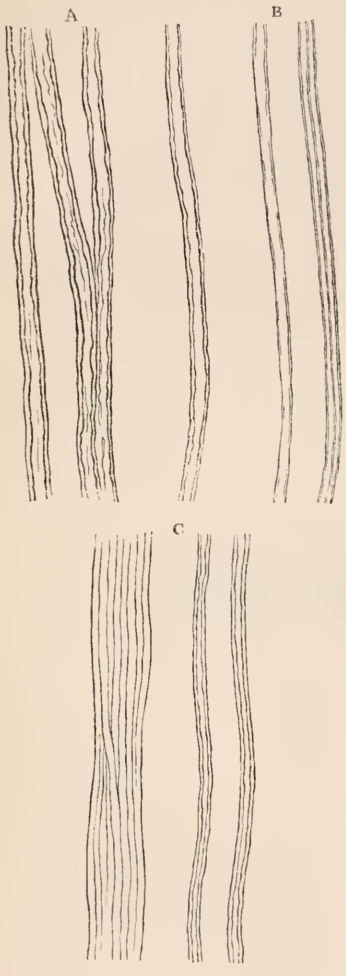
As regards the further course of the fibres which are derived by the sympathetic from the cerebro-spinal system, Valentin†, holding the view that this nerve is entirely composed of such fibres, believed that on joining the

* Nerven-Physiologie in Wagner's Handwörterbuch, Eilfte Lieferung, p. 609.

† De Functionibus Nervorum, § 152. 155. See also Quain's Anatomy, by Sharpey.

main or gangliated cord they all run in a downward direction towards the pelvic ex-

Fig. 294.



Fibres from the root of intercostal nerve of a Rabbit.

Towards C (in *fig.* 293.), the nerve chiefly consisted of fibres similar to those indicated by B; towards *b* it consisted chiefly of broad fibres, A; C fibres from the communicating branch. (Mag. 250 diam.)

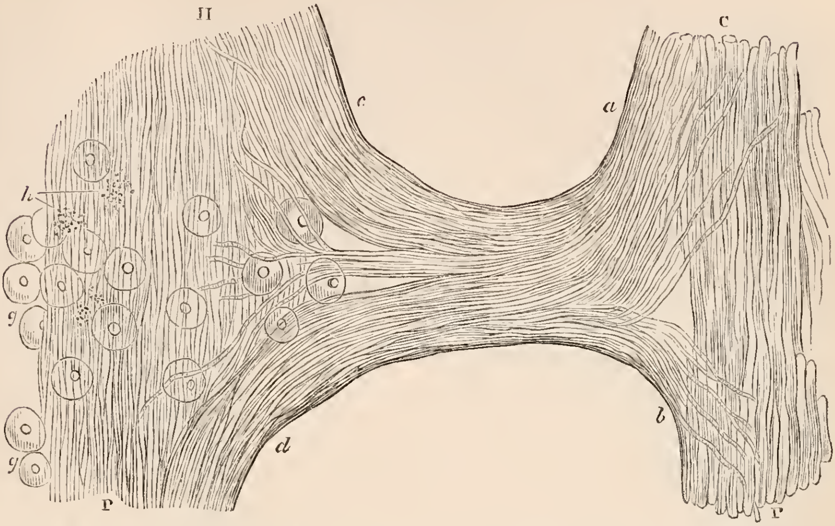
tremity, none passing upwards towards the cephalic extremity. After thus running for a greater or shorter distance in the main cord, they then pass off from it in the peripherical branches, the point at which they leave the cord being always situated lower down than the point at which they entered it. This arrangement was termed by him the *lex progressus*: he endeavoured to support it by experiments on the motory action of the fibres contained in the sympathetic, showing that when different parts of the cerebro-spinal axis, as well as the rami communicantes, are irritated, the contractions produced in the viscera follow a certain order, which favours the opinion that the fibres are disposed in the manner he states. This view is opposed by Bidder and Volkmann*, on the ground that it is at variance with what is actually observed in regard to the course of these fibres on joining the sympathetic. On examining with the microscope the communicating branch at its point of junction with the sympathetic, they find that in so far as it consists of cerebro-spinal fibres it divides into two portions, one of which is directed downwards in the direction of the pelvis, while the other passes upwards towards the head. In small animals, such as the rabbit or mouse, it is not difficult, when one of the thoracic communicating branches is examined with the microscope, to observe that the fibres are disposed in the manner in which Volkmann and Bidder describe, some passing upwards, others downwards into the main cord of the sympathetic, and in which they may be traced for some distance, and, according to Kölliker, into the peripheral branches. That they all gradually pass off from the main trunk of the sympathetic into its peripheral branches is probable, as Kölliker observes, from the fact that most of these contain a greater or smaller number of fibres resembling those in question.

Peripherical Distribution. — The different branches of the sympathetic contain the same structures as those which have been already described as constituting the main trunk of the nerve, viz. broader and finer tubular nerve-fibres and fibres of Remak. These, however, vary in the proportion in which they are present in the different branches. In the whiter branches of the sympathetic, such as the splanchnic nerves, the number of tubular nerve-fibres, as compared with the number of the fibres of Remak, is much the same as in the main trunk. The grayer branches, on the other hand, such as the ascending or carotid branches of the superior cervical ganglion, the nervi molles as well as the arterial branches generally contain a large number of the fibres of Remak. Many of them appear to be entirely composed of these and fine tubular fibres. The nerves which are distributed to the heart are also chiefly composed of fine tubular fibres and fibres of Remak. In the heart of the sheep many of the branches which run along the surface of the ventricles are chiefly composed of the latter variety of fibres, there being few tubular fibres present. As already mentioned, numerous small ganglia have been described by Remak as occurring on the cardiac nerves, both on the surface and also in the substance of the organ. As regards the fibres on the inner surface of the heart, they cannot be distinguished by the naked eye. If, however, the lining membrane is dissected carefully off from the muscular substance, and then, after addition of diluted solution of soda, examined with a power of 250 diameters, they may frequently be observed. They consist of tubular nerve-fibres belonging to the finer variety, and are arranged

* Die Selbständegkeit, &c., p. 31.

in bundles containing from six to three nerve-tubes forming a widely-meshed network. The rami intestinales present much the same characters as the nerves of the heart. Many of

Fig. 295.



Communication between the sympathetic and third spinal nerve in the Frog, showing the arrangement of the fibres of the communicating branch at its points of junction with the spinal and sympathetic nerves.

H P, sympathetic nerve; H, cephalic side of the same; P, pelvic, C P, spinal nerve; C, its central, and P its peripheral end. *a*, portion of communicating branch running centrally; *b*, portion of ditto running pheripherically; *c* and *d*, fibres of the ramus communicans passing upwards in the direction of the head, and downwards towards the pelvis; *g*, *g*, ganglion-cells; *h*, pigment. (*After Bidder and Volkmann.*)

the fibres seem to become lost in the muscular coats of the intestine; a few slender twigs, particularly in the stomach, can be traced through these to the mucous or submucous coats. The nerves of the unimpregnated uterus also contain a considerable number of the fibres of Remak. In the impregnated uterus of the cow, some of the twigs which run along the cervix of the organ consist almost entirely of fine tubular nerve-fibres; in others the fibres of Remak are more numerous than the tubular nerve-fibres. Ganglia have been observed by Remak on the nerves distributed to the muscular substance of the cervix uteri in the pig. Small ganglia are also present in the impregnated cow's uterus, both on the nerves passing to the organ and also in the twigs which pass upwards along the posterior wall of the cervix of the uterus. Some of them contain as few as from six to nine ganglionic corpuscles: they seem to be more numerous, and are larger near the point where the cervix uteri becomes continuous with the vagina. Divisions of the fine tubular nerve-fibres have been observed by Kilian*; he describes a fibre belonging to the finer variety as dividing into two branches, and each of these, after running a short distance, as again dividing. As regards the nerves of the urinary bladder, in that of the ox they are very numerous, especially towards the neck and posterior aspect of the organ, and present a more or less white appearance. Some run beneath the peritoneal coat, others between the deep and superficial layers of muscular fibres; and some may be traced through these to the mucous coat. At first the branches contain both broad and fine tubular fibres: in their farther course, only fine fibres appear to exist. There are present, especially towards the cervix of the organ, a number of small ganglia similar to those in the uterus. Ganglia have also been described by Müller as occurring on the nerves distributed to the cavernous tissue of the penis.

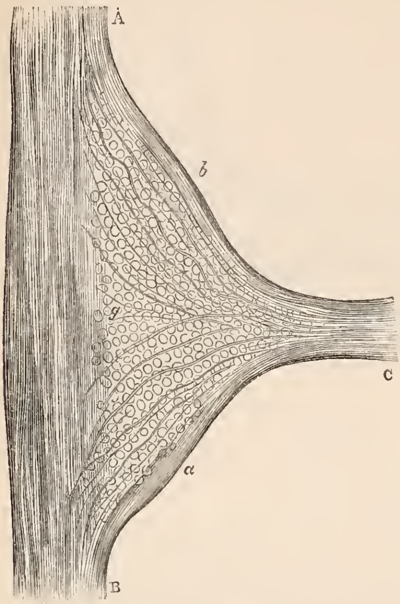
The branches of the sympathetic which pass to the different glandular organs also consist chiefly of fine nerve-fibres and fibres of Remak. In general there are more or fewer fibres belonging to the broad variety also present. In the substance of the organs they run in company with the blood-vessels and with the ducts of the glands, and appear to be chiefly distributed to these: at least no nerve-fibres have as yet been discovered running separate from the vessels or ducts in the parenchyma of the organ. In the finer ramifications of the nerves, the broader tubular fibres gradually disappear. The fine fibres also lose their distinct dark margins, and become pale and more or less indistinct. Their exact mode of termination has not been determined. Pappenheim, however, describes the nerves of the kidney as terminating in a looped arrangement. Small ganglia occur on the nerves distributed to

* Henle and Pfeuffer's Zeitschrift, p. 222.

Supp.

many of the glands: they have been seen by Ludwig on the nerves of the kidney; also by

Fig. 296.



Fourth thoracic ganglion of Rabbit; showing the course of the fibres contained in the communicating branch after reaching the sympathetic.

A B, main cord of sympathetic; A, cephalic, B, pelvic extremity; C, communicating trunk; *g*, ganglionic corpuscles; *a*, portion of the fibres in the communicating branch passing towards the pelvic extremity; *b*, ditto passing towards the head. (*Magnified* 70 *diameters.*)

Pappenheim on the nerves distributed to the supra-renal capsules. Schaffner* has also observed ganglionic corpuscles from which nerve-tubes proceeded, in the substance of the lymphatic glands. Small ganglia have also been described by Remak as occurring on the nerves distributed to the bronchi: they have also been observed by Kölliker. The latter observer believes that he has seen nerve-tubes arise from them.

From the observations of Purkinje* it would appear that numerous fibres of the sympathetic pass to the cerebro-spinal membranes. In the dura mater of the cranium he describes the nerves as most abundant in the neighbourhood of the trunks of the three meningeal arteries. Most of them accompany the vessels; but there are also others which leave them and ramify in the membrane. In the pia mater of the cerebellum the nerves which branch separately from the arteries are not so numerous as in the pia mater of the cord. The nerves in the pons and cerebrum belong exclusively to the arteries: no trace of nerve-fibres was seen in the choroid plexuses. Around the vena Galeni magna they form a dense plexus which passes into the tentorium cerebelli, and seems to belong to it rather than to the venous system. The nerves in the pia mater of the cord unite with those of the cerebellum and pons. In the pia mater of the spinal cord the nerves are more abundant than in any other part of the cerebral membranes; they run singly or in bundles of two and three; others contain from thirty to fifty filaments. Sometimes fibres leave the bundles, forming loops and returning to the same or to a different bundle. The largest bundles are situated near the anterior spinal artery, which they entwine; and some pass from this into the process of the dura mater in the anterior fissure, and form loops in the same. Other large bundles, running mostly in a longitudinal direction, are situated near the ligamentum dentatum and posterior median line of the cord. Near the origins of the spinal nerves the bundles of sympathetic fibres are not so numerous and are also smaller. Some of these fibres spring from the cerebro-spinal nerves, and enter with the arteries through the intervertebral foramina. In the peritoneum nerve-fibres have been described by Bourgery* as existing in considerable numbers. They have also been observed by Luschka.† Nerve-fibres are also abundant in the periosteum, both that which invests the shafts of the bones and the articular extremities of the same, as shown by the observations of Pappenheim.‡ They are chiefly situated in the outer part of the membrane, and either run in company with the vessels or are situated upon them. They terminate in loops. Nerves also exist, according to the same author, in the cellular tissue which surrounds the ligaments, penetrating these along with the arteries, and terminating in a series of plexuses and loops. In the tendons they are also sometimes present. Wherever (according to Pappenheim) vessels pass to ligaments or tendons, nerves pass also.

Development. — In the cow's embryo of $8\frac{1}{2}$ lines in length, the gangliated cord of the sympathetic in the thorax was observed, by Kiesselbach §, on either side of the spinal column in the form of a thick cord, presenting numerous inequalities. In the pig's embryo, eight lines in length, it presents, according to Valentin, the same aspect. It seems, at this period, to consist of a series of small ganglia placed almost in juxta-position to each other, the interval between the individual ganglia not being very distinct. In another embryo, measuring about thirteen lines in length, Bischoff found the gangliated chain distinctly formed, not only in the thoracic, but also in

* Vermischte Beobachtungen in Henle und Pfeuffer's Zeitschrift, band vii. p. 177.

† Müller's Archiv. 1845.

* Comptes rendus, 1845, p. 566.

† Luschka, die Structur des Serosen Häute des Menschen, quoted in Canslatt's Jahresbericht.

‡ Müller's Archiv. 1843.

§ Disser. Syst. Histor. Formationis ac Evolutioni Nervi Sympathici: Münich, 1835; quoted in Bishoff's Entwikelung und geschichte, French Translation.

the cervical region: the superior cervical ganglion presented the aspect of a small round nodule. In the cow's embryo, measuring about $1\frac{1}{2}$ inches in length, I found the ganglia in the cerebral and spinal nerves, as well as those of the sympathetic, very distinct. The superior cervical ganglion of the sympathetic appeared as a small reddish grey mass, of an irregularly oval form, measuring about $\frac{1}{25}$th of an inch in its longest diameter, soft and breaking down readily. It was situated close to the pneumogastric, a narrow indistinct whitish line passing downwards from the lower part of the ganglion to that nerve. The lower cervical ganglion presented a more elongated form, and appeared to be prolonged into the first thoracic: the other thoracic ganglia appeared as minute greyish particles between the heads of the ribs, and measuring about $\frac{1}{30}$th of an inch in diameter. The ganglia in the lumbar and sacral regions presented in general a more elongated form, and were not so distinctly separated from one another: the connecting cord, especially in the sacral region, being short and thick, and looking as if it were a prolongation of the one ganglion into the other. None of the branches which are sent inwards from the sympathetic cord, nor the ganglia occurring upon them, could be accurately distinguished from the surrounding structures. As regards the ganglia occurring on the cerebral and spinal nerves, they were much more distinct than those of the sympathetic. The Gasserian ganglion presented the form of a greyish white body, situated beneath the still soft and transparent dura mater: it measured about $\frac{1}{15}$th of an inch in diameter, and presented an irregularly oval or triangular shape. It appeared to consist of several opaque portions, separated from one another by an intermediate more or less transparent substance, thus presenting the appearance of being composed of several minute lobules. The ganglia on the posterior roots of the spinal nerves were also very distinct: they were arranged along the interior of the spinal canal, on each side, and rather anteriorly towards the bodies of the vertebræ, and concealed by the spinal cord. They presented an oblong or oval shape, measured about $\frac{1}{25}$th of an inch in length and about $\frac{1}{30}$th in breadth, and presented the same characters in regard to colour, &c., as the Gasserian ganglion.

Fig. 297.

Sixth thoracic ganglion of the left side, from the sympathetic of a Rabbit, treated with soda, and magnified forty diameters.

Tr, main cord of sympathetic; Rc, Rc, communicating branches, each dividing into two portions; Spl, splanchnic nerve; S, small nerve proceeding probably to the blood-vessel; G, ganglion-cells and fibres, passing into the main cord of the sympathetic. (*After Kölliker.*)

In embryos from seven to eight inches in length, the superior cervical ganglion presents the same oval shape and reddish grey appearance as before: it is larger, however, measuring about $\frac{1}{12}$th of an inch in its long diameter: it consists, as before, of a number of opaque round or oval portions: the intermediate substance exists in much smaller quantity. It is surrounded by a highly vascular sheath. From its lower part the communicating cord is seen passing downwards for a short distance, when it is applied to the trunk of the pneumogastric. The cord presents a flattened aspect, and is of a greyish red colour. The ganglia in other regions of the body, as well as the intermediate cord, are well formed, and much larger than before. The first sacral ganglion of either side appears to be amalgamated into a single ganglion situated in the medial line.

The splanchnic nerves and solar plexus, as well as its offsets, are distinctly visible. The rami communicantes are also present; so also the plexus on the abdominal aorta and epigastric plexuses. The ganglia on the cerebral and spinal nerves present the same characters as before, with the exception that they are considerably larger.

In embryos measuring seventeen or eighteen inches in length, not only can the parts which have been already mentioned be distinctly seen, but also most of the peripherical branches of the sympathetic. The superior cervical ganglion presents, as before, a more or less oval shape, and measures about $\frac{1}{6}$th of an inch in its long diameter. It has still the appearance of being composed of a number of round or oval opaque greyish-white masses: there appears, however, to be very little of the intermediate transparent substance present. Its sheath is very vascular, and numerous vessels also pass into the interior of the ganglion between its lobules: it is possessed of considerable consistence. Its branches of communication with the different nerves are also distinctly seen: they have a more or less greyish red appearance. The lower cervical ganglion presents an irregularly oblong shape, about $\frac{1}{5}$th of an inch in length and $\frac{1}{10}$th of an inch in thickness, and still has the appearance of being prolonged downwards into the first thoracic ganglion. The thoracic ganglia are much smaller, measuring about $\frac{1}{10}$th of an inch; and are more or less triangular in shape, presenting the lobulated aspect above described. The connecting cord between the different ganglia has a reddish grey colour, is flattened, measuring about $\frac{1}{25}$th of an inch in breadth, and presents the appearance of consisting of distinct bundles of fibres. A portion of these can be traced over the surface of the ganglia, others appear to sink into them, while a considerable number can be traced into the rami communicantes. The latter are very distinct; some of them in the thoracic region appear to be almost as thick as the cord of the sympathetic itself, and all of them present the same greyish red appearance. On turning inwards to the sympathetic, many of their fibres are seen to be prolonged into the main cord of the sympathetic, and merely run along the sides of the corresponding ganglia: these pass both upwards towards the head, and downwards in the direction of the pelvis. They join the spinal nerves at the point where the anterior and posterior roots become united into a common trunk. By far the greater portion of the fibres in the rami communicantes run inwards towards the spinal cord.

The splanchnic nerve, which is about $\frac{1}{4}$th of a line in thickness, has a whiter aspect than the main cord of the sympathetic.

The nerves on the surface of the heart are very numerous and distinct, presenting the same arrangement as has been already described. The cœliac and epigastric plexuses are also large; the latter containing several ganglia. There are also several small ganglia in the plexus upon the abdominal aorta.

The ganglia on the cerebral and spinal nerves present much the same appearance as those in the animal after birth, only they are softer and have a redder colour.

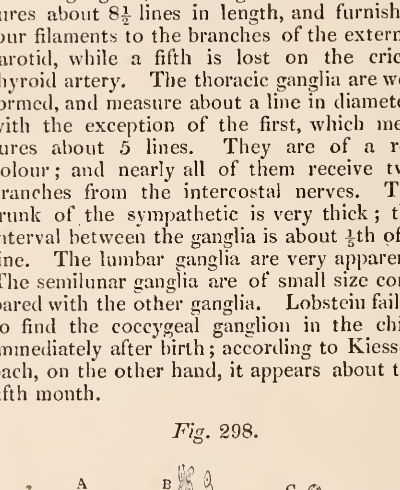
As regards the development of the sympathetic in the human subject, it would appear from the observations of Lobstein*, that in the embryo of the 14th week, about three inches in length, the main cord of the nerve was very apparent. In the chest it constituted a thick cord of a red colour, the ganglia being closely approximated towards one another. The superior cervical ganglion was very well formed, and about two lines in length, and half a line in thickness. The great splanchnic nerve existed as a very delicate filament: the semilunar ganglia were almost imperceptible.

In an embryo male, about five months, old and measuring six inches in length, Lobstein found the trunk of the sympathetic very distinctly developed. It constituted an uninterrupted cord extending from the base of the cranium to the pelvis. The superior cervical ganglion was rounder than in the adult: it was three lines in length, and about half a line in thickness. The greater splanchnic nerve was very distinct, but very delicate, and arose by three roots. The semilunar ganglia were small, indistinct, and measured only about half a line in their greatest diameter. They were adherent to the supra-renal capsule and to the vessels. The thoracic ganglia, with the exception of the first, constituted little enlargements about half a line thick. According to Kiesselbach, the solar ganglia do not make their appearance until about the 7th month. At the 5th month, he found the ophthalmic and submaxillary ganglia formed; and about the 6th month, the spheno-palatine ganglion appears; and in the 5th month, according to the same author, the communicating branches between the sympathetic and cerebro-spinal system appear.

In the fœtus of eight months, the superior cervical ganglion, according to Lobstein, measures about five lines in length, and a line and a half in breadth. The greater splanchnic nerve is very distinct, but very fine, and terminates in an imperfect semi-lunar ganglion.

In the fœtus, at the full period, the superior cervical ganglion, according to Lobstein, measures about $8\frac{1}{2}$ lines in length, and furnishes four filaments to the branches of the external carotid, while a fifth is lost on the crico-thyroid artery. The thoracic ganglia are well formed, and measure about a line in diameter, with the exception of the first, which measures about 5 lines. They are of a red colour; and nearly all of them receive two branches from the intercostal nerves. The trunk of the sympathetic is very thick; the interval between the ganglia is about $\frac{1}{5}$th of a line. The lumbar ganglia are very apparent. The semilunar ganglia are of small size compared with the other ganglia. Lobstein failed to find the coccygeal ganglion in the child immediately after birth; according to Kiesselbach, on the other hand, it appears about the fifth month.

Fig. 298.



A, ganglionic corpuscles from the Gasserian ganglion of a calf $1\frac{1}{2}$ inch in length; B, nerve-fibres from the same; C, from one of the thoracic ganglia of the sympathetic in the same animal.

With respect to the minute structure of the ganglia and nerves in the fœtus, the Gasserian ganglion in the fœtal calf, $1\frac{1}{2}$ inch in length, consists of the following elements: 1st, bodies measuring from the $\frac{1}{4000}$th to the

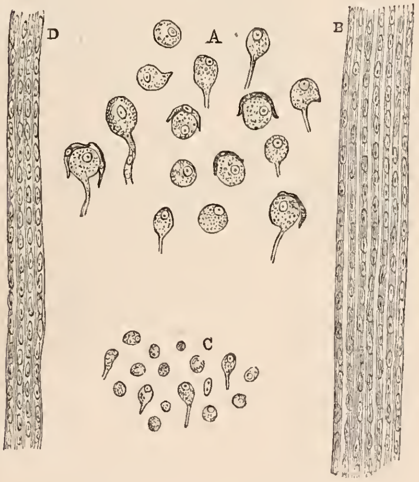
* De Nervi Lympathici humani fabricâ, usu, et morbis, cap. iii. p. 47.

$\frac{1}{3500}$th of an inch in diameter, and presenting a slightly granular surface (most of them are round; others have more or less an oval shape); 2nd, distinct cells measuring from the $\frac{1}{2000}$th to the $\frac{1}{1200}$th of an inch in diameter: they contain a finely molecular fluid, and also a nucleus. The latter, which is frequently situated towards one side of the cell, is round and granular, and generally contains a nucleolus. With the exception of their smaller size, they resemble ordinary ganglionic corpuscles. The nerves in the ganglion present the aspect of flattened bands of blastema, consisting almost entirely of corpuscles resembling those first described, arranged close together in linear series in a somewhat granular matrix. They vary in breadth considerably. The ganglia on the posterior roots of the spinal nerves present the same structure.

The sympathetic ganglia appear to be entirely composed of structures similar to those first described, imbedded in a more or less granular transparent blastema.

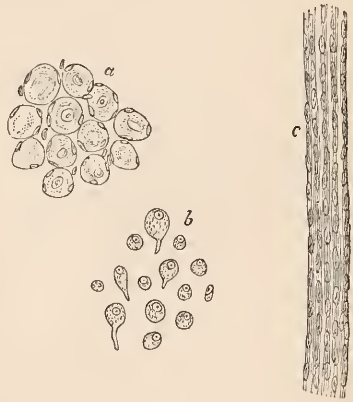
In embryos of 6 to 8 inches in length, the sympathetic ganglia still contain a large number of corpuscles similar to those in earlier embryos. There are also present a number of bodies larger than these, and consisting of a distinct cell-wall inclosing, besides a nucleus, a finely-granular fluid. They are commonly round; some are more or less egg-shaped. The nucleus in the latter is generally situated towards the wider extremity of the cell, while its narrow end is prolonged into a delicate, granular process about the $\frac{1}{5000}$th of an inch in breadth. The nerves in the ganglia do not differ much in appearance from those in the Gasserian ganglion of the embryo of $1\frac{1}{2}$ inches in length. The sympathetic cord and branches present the same structure. In the ganglia of the cerebro-spinal nerves, the ganglionic corpuscles are larger and more distinctly formed than in the sympathetic ganglia. Many of the cells have processes similar to those above described; and in several of these, at a short distance from the corpuscle, there is a small oval nucleus such as Kölliker describes in the human embryo of 16 inches. The nerves belonging to the cerebro-spinal system are also much further developed than those in the sympathetic. Those in the brachial plexus present the appearance of being composed of a slightly-granular transparent blastema, marked by longitudinal striæ, and containing embedded in it oval granular nuclei. The striæ are arranged parallel to one another, and evidently correspond to the margins of the nerve-fibres. The nuclei are arranged at intervals, and occupy the entire breadth of the fibres. There is no trace of the white substance of Schwann.

Fig. 299.



A, Ganglion-corpuscles from the Gasserian ganglion of a calf 7 inches long; B, nerve-fibres from the brachial plexus of the same animal; C, from the superior cervical ganglion of the sympathetic; D, nerve-fibres from the main cord of the sympathetic in the thorax.

Fig. 300.

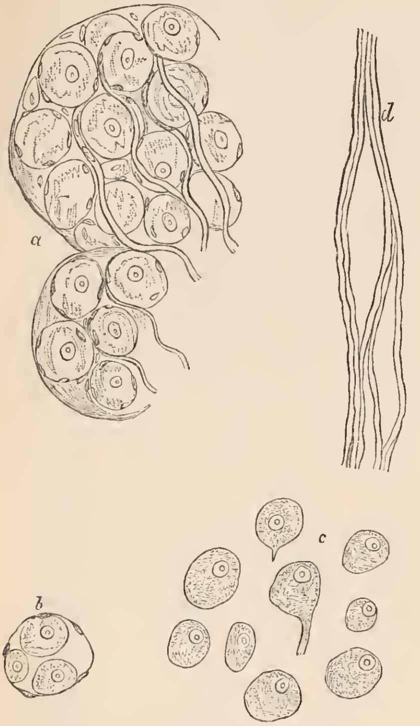


From the semi-lunar ganglion of a Calf 18 *inches long.*

a, portion of ganglion; *b*, corpuscles isolated; *c*, nerve-fibres connected with the ganglion.

In the sympathetic ganglia of embryos measuring 18 or 19 inches in length, there are still present a considerable number of granular corpuscles measuring from the $\frac{1}{4000}$th to the $\frac{1}{2500}$th of an inch in diameter, similar to those already described. They are chiefly composed, however, of cells resembling those in the ganglia after birth, only smaller and more delicate. The nerve-fibres in the ganglia have much the same appearance as those already described in the brachial plexus of embryos from 6 to 8 inches in length. In the ganglia occurring on the posterior roots of the spinal nerves, the Gasserian ganglion, and the ganglion on the trunk of the pneumo-gastric, the ganglionic corpuscles differ from those in the perfect animal only in point of size. Most of the nerve-fibres connected with the ganglia present the same tubular character as the perfect nerve-fibre. The nerve-fibres in the roots of all the cranial nerves present the distinctly tubular character also ; in those of the 3rd, 4th, and 7th, the double contour is more

Fig. 301.



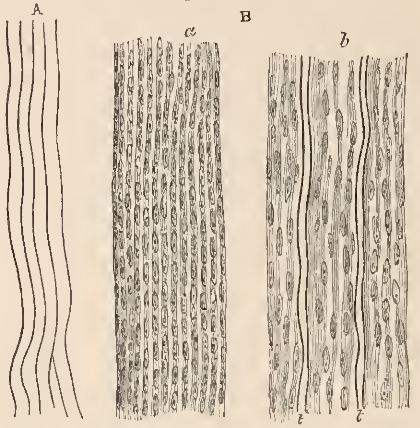
From the Gasserian ganglion of the same animal as the preceding figure.

a, portion of ganglion with corpuscles *in situ*; *b*, three corpuscles included within a single capsule; *c*, ganglionic corpuscles freed from their capsules; *d*, nerve-tubes connected with the ganglion.

or less distinctly visible. The optic nerve consists of fine tubular fibres mingled with small round or oval bodies. The nerve-fibres in the brachial plexus also present the character of perfect tubular fibres; they are narrower than in the adult animal. So also the fibres in the trunk of the pneumogastric; throughout the entire extent of the trunk of this nerve, in the neck and upper part of the thorax, there were embedded amongst its fibres ganglionic corpuscles similar in their character to those occurring in the ganglia of the cerebro-spinal nerves. Sometimes a single corpuscle lay imbedded in a bundle of nerve-fibres; in other parts two were seen, one situated above the other; and in some parts there were as many as six, all arranged close together in linear series; some of them were seen to give off a nerve-tube at one extremity; and once or twice the corpuscle was seen to be connected with two such, one passing towards the centre, the other in the direction of the periphery.

The main cord of the sympathetic appears to be entirely composed of fibres presenting the nuclear character, similar to those already described in connection with its ganglia, and representing an early stage of the development of the cerebro-spinal nerve-fibres. Addition of dilute solution of soda brings into view a few tubular nerve-fibres similar to those in the spinal nerves. The splanchnic nerves present the same structure as the cord of the sympathetic, containing a few tubular nerve-fibres, but being chiefly composed of the other structures. In one of the nerve-filaments from the surface of the right ventricle of the heart,

Fig. 302.



A, nerve fibres from the brachial plexus of a Calf 18 inches long. B. *a*, nerve-fibres from the sympathetic cord in the thorax; *b*, the same treated with dilute solution of soda, showing the presence of tubular nerve-fibres, *t t*, similar to those in the cerebro-spinal nerves.

there were no tubular nerve-fibres present; it consisted entirely of structures similar to those already described. As regards the communicating branches, all of them contained more or fewer tubular nerve-fibres ; some appeared to be entirely composed of these, while others consisted chiefly of the partially-developed nerve-fibres. The difference in point of structure between the fibres in the cerebro-spinal nerves and those occurring in the sympathetic is at this period of embryonic life very remarkable : while the former present for the most part the tubular character of the perfectly-formed nerve-tube, the latter appear to consist of a mass of blastema with numerous granular nuclei imbedded in it, corresponding, in short, to the fibres of the cerebro-spinal system in the fœtus measuring 6 to 8 inches in length. This also applies, though perhaps in a less degree, to the ganglia of the sympathetic as compared with those on the cerebro-spinal nerves, the latter being more fully developed, both as regards their ganglionic corpuscles and nerve-fibres, than the former.

As regards the further development of the nerve-fibres of the sympathetic, it would appear, from the observations of Volkmann and Bidder, that they undergo little further change during the whole period of embryonic life.

At least, in embryos near the full time, they observed little change in the sympathetic nerve-fibres.

It has been already stated that in the sympathetic of embryos of 18 or 19 inches in length there are some tubular fibres present; these, probably, are to be regarded as fibres sent from the cerebro-spinal system.

PHYSIOLOGY.—The actions which take place in the animal body may be divided into two classes. Those which are included in the one class are entirely under the guidance of volition; those which belong to the other not only take place independently of any effort of the will, but are also more or less completely removed beyond its control. The movements which occur in the muscles of the limbs, and in most of the muscles of the trunk, form examples of the former; while the movements of the internal muscular organs, such as those of the heart, intestinal canal, and genito-urinary organs, afford examples of the latter. To the latter also belong the acts of nutrition, secretion, &c., commonly termed the vegetative processes. Several of the latter, as the movements of the heart, go on without interruption during the entire life of the individual; while others, as the movements of the intestinal canal, take place at irregular intervals, depending apparently on the application of external stimuli to the free surfaces of the organs in which they are manifested. The exercise of the former class of actions is moreover attended by sensation; that of the latter, in the normal condition, not. The impressions which are constantly being made by the blood upon the inner surface of the heart and vessels never reach the sensorium; we are also insensible to the impressions made by the food upon the free surface of the intestinal canal, as well as to the contractions thereby induced. In like manner, the acts of nutrition and secretion take place entirely without our knowledge. The feeling of weariness also which ensues after exertion of the voluntary muscles, is never felt so far as the heart is concerned, although its action is constant, and just as little in regard to the other organic muscles.

The organs in which the former class of actions takes place are supplied with nerves which proceed directly from the brain and spinal cord; those whose actions belong to the second class derive their nerves chiefly from the sympathetic.

Guided by this difference in character between the vital phenomena, Bichat divided life into animal and vegetative; the former characterised by the circumstance of its phenomena coming within the range of sensation and volition; the latter including those acts which are more or less completely removed beyond the sphere of the will and of the consciousness. In accordance with this division, he also separated the nervous system into two portions: the one corresponding to the cerebro-spinal system, presiding over the functions of animal life; the other corresponding to the sympathetic, presiding over the involuntary movements, and over the processes of nutrition and secretion, or functions of vegetative life. The sympathetic and its ganglia are, according to the views of Bichat, entirely independent of the cerebro-spinal system of nerves. The various ganglia of the sympathetic he regarded as so many distinct nervous centres, each presiding over the actions of the parts to which it sends nerve-filaments, and each discharging its functions without any relation to the brain or the spinal cord. The involuntary nature of the processes which take place in organs supplied by the sympathetic, as well as the circumstance that the normal impressions which are made upon the free surfaces of these do not reach the sensorium, rendered the views of Bichat highly probable. In diseases of the brain and spinal cord, as in tetanus and chorea, where the muscles supplied by cerebro-spinal nerves are all thrown into a state of more or less violent contraction, the muscular organs which derive their nerves from the sympathetic, such as the heart, continue their movements as before. So also a stimulus applied to the brain or spinal cord, causes contractions in the muscles which derive their nerves from these parts, but does not, according to Bichat, produce any effect on the movements of parts which are supplied by the sympathetic. The fact that embryos in which the central masses of the nervous system are wanting may reach an advanced stage of development, showed that the processes of vegetative life might go on perfectly, independently of the influence of the cerebro-spinal system, while the circumstance that in these the sympathetic system of nerves was always present, and in a high state of development, seemed at the same time to indicate the connection subsisting between it and the processes in question.

The views of Bichat were generally adopted by physiologists until comparatively recent times, when they were ably combated by Valentin, who endeavoured to establish the doctrine, commonly held before the time of Bichat, that the sympathetic and cerebro-spinal nerves do not constitute two distinct and independent systems, but that the former is dependent upon the latter for all its properties, and is in this respect to be regarded as one of the cerebro-spinal nerves. The involuntary and apparently spontaneous nature of the movements which take place in organs supplied by branches of the sympathetic, affords no argument, according to Valentin, for supposing that their action is not regulated by the brain and spinal cord, or that the sympathetic is independent of these parts of the nervous system, inasmuch as the same character is also presented by the movements of certain organs which are undoubtedly supplied by cerebro-spinal nerves. This, for example, is the case with the rhythmical movements of the muscles of respiration. Again, there are organs which are supplied by nerves of cerebro-spinal origin, and which notwithstanding resemble the organs supplied by the sympathetic in the circumstance that the normal impressions which are made upon them do not reach the sensorium. Thus, the greater part of the mucous membrane which lines the bronchial tubes, as well as that of the œsophagus, receives its nerves from the eighth pair; the lacrymal glands receive filaments from the fifth nerve ; and from the fifth and seventh nerves fibres are distributed to the salivary glands : and yet all these organs present the same relations in regard to sensibility as the pancreas or other glands which derive their nerves from the sympathetic. The fact of certain parts being beyond the control of the will, and from which the ordinary impressions they receive are not conveyed to the sensorium, does not so much depend on any peculiarity in the nerves with which they are supplied, as upon their anatomical constitution. Such is the case, for example, with the muscular fibres presenting the same characters as those which are found in the walls of the ducts of the various glands, as well as with those which are present in the coats of the blood and lymphatic vessels. That the impossibility of influencing these structures by any effort of volition, as well as the fact of their being removed from the sphere of sensation, do not depend on any peculiarity in the properties of their nerves, is shown, Valentin says, by the fact that the greater part of the nerves for the salivary glands are derived, as above stated, from the fifth and seventh cerebral nerves. The same thing also holds true, according to him, of the mammary glands, the nerves supplied to which proceed chiefly from the supra-clavicular and intercostal nerves. As regards the argument which is drawn in favour of the views of Bichat, from anencephalous fœtuses, Valentin remarks that there is no evidence to show that in the development of the various organs in the fœtus nervous influence is at all concerned ; and, moreover, that the phenomena of growth and nutrition are not dependent on the sympathetic is shown by the circumstance of few or no sympathetic fibres being sent to the extremities. The sympathetic is moreover capable of transmitting stimuli to and from the cerebro-spinal centres, in the same manner as the ordinary nerves arising from these, though in a less degree; stimulus applied to the spinal cord being capable of exciting contractions in the heart and intestinal canal, while on the other hand stimuli applied to the latter may also be transmitted to the former. This is shown by the severe pain which is felt in organs supplied by the sympathetic, when affected with disease, as well as by the circumstance that irritations of the intestinal canal not unfrequently give rise to contractions in the muscles of animal life : as is not unfrequently the case with children, when the presence of worms in the intestinal canal gives rise to impressions which are conveyed along the centripetal nerves to the spinal cord, and are there transferred to the motor nerves which pass to the voluntary muscles, exciting them to contractions. As already stated, Valentin believes that all the true nerve-fibres which are present in the sympathetic, are derived from the brain and spinal cord ; on entering the sympathetic they pass through a greater or smaller number of its ganglia, and are then distributed to the different organs, in the same way as the ordinary cerebro-spinal nerves. The sympathetic is therefore, according to him, a cerebro-spinal nerve, possessed of the same properties, and deriving these from the same source as the other cerebro-spinal nerves ; the only peculiarities in the sympathetic being its numerous points of origin, as well as the large number of ganglia which it presents. Similar views are also held by Longet*, and others.

After the discovery of the gelatinous fibres in the sympathetic, it was held by some, that while motion and sensibility in the organs supplied by this nerve depended upon the tubular nerve fibres sent to them through the medium of the branches of the sympathetic by the brain and spinal cord, the processes of nutrition depend upon the gelatinous or proper sympathetic fibres. Moreover, as these fibres are found in the cerebro-spinal nerves also, it is supposed that they pass to the extremities along with the cerebro-spinal nerves, where they in like manner preside over the nutrition of these parts. According to these authors, the ganglia are so many centres, from which nerve fibres, possessing peculiar properties, pass off in different directions ; some to the viscera, others to the extremities, along with the cerebro spinal nerves, and by means of which the nutritive processes are regulated. Thus, while the internal viscera receive sensory and motor nerve fibres from the brain and spinal cord, they, as well as the organs of animal life, receive the nerve fibres which regulate the nutritive processes from the sympathetic. Such seems to be the view of Remak †, R. Hall ‡, and others.

Volkmann § adopts the same view as was held by Bichat, regarding the sympathetic as constituting a system of nerves distinct from and independent of the cerebro-spinal system. Under the term sympathetic, he includes not only the sympathetic, commonly so called, but also the ganglia which occur on the posterior roots of the spinal nerves, as well as those which are present on several of the cerebral nerves. All the finer nerve fibres are regarded by him as sympathetic fibres. These originate in the different ganglia ; some of them pass inwards to the viscera, over whose movements and nutrition they preside, while others pass along with the cerebro-spinal nerves to the extremities, and serve as the nerves of nutrition to these parts. Each of the ganglia he regards as a nervous centre.

* Anatomie et Physiologie de Système Nerveux, tome ii. p. 569. et seq.

† Observat. Anat. et Microscop. de Systemat. Nerv. Structurâ, Berlin, 1838.

‡ Edinburgh Medical and Surgical Journal, July, 1846, &c.

§ Wagner's Handwörterbuch der Physiologie Zehnte Lieferung, p. 499.

By the term centre, Volkmann seems to mean an organ which serves as a regulating apparatus, and by which several separate and simple acts are combined into a single complex organic act. The contraction of a muscle is a simple act; in the act of respiration we have the contractions of many muscles combined into a single complex act, their combination being dependant on a power situated in the medulla oblongata, which part of the nervous system is therefore termed their central organ. The question then in regard to the independence of the sympathetic is, whether, in the sphere of the organic nerves, there be such combinations, and whether these have their centre in the brain and spinal cord, or in the sympathetic. The brain is the centre of all psychical acts; it is therefore evident that the sympathetic, in so far as regards all the phenomena of sensation occurring in its sphere, must be regarded as dependent on the brain. But after the brain and spinal cord have been destroyed, does the sympathetic still remain active, and in such a state of activity as implies the co-operation of a central organ? Muscular motion implies the activity of the motor nerves, and the activity of those muscles which are supplied by the sympathetic must imply the activity of sympathetic nerve fibres. The action of the heart, however, as well as the circulation, sometimes continues for weeks after the destruction of the central masses of the nervous system. Thus Bidder removed with great care the arches of the second cervical vertebra, so that little blood was lost during the operation, and then completely destroyed the spinal cord. Frogs treated in this way often lived six weeks, sometimes ten, the circulation, as seen in the web of the foot, remaining at the same time active, and not differing from that in uninjured frogs. The heart beat powerfully and quickly: in a freshly-killed frog, in winter, the heart pulsated thirty-five times in the minute; while in a frog, the spinal cord of which had been destroyed twenty-six days previously, the pulsations were forty per minute. When the brain and spinal cord were destroyed, the medulla oblongata being left, frogs were retained in life until the sixth day; and when the entire central organs of the nervous system were removed, they lived until the second day; the rapidly ensuing death in the latter case being due, according to Volkmann, to the effects produced upon the respiration. Within a few weeks after the destruction of the spinal cord the muscles of animal life were found to have lost their irritability in a marked degree, and still later no contraction could be produced in them by application of chemical or mechanical stimuli; the heart, however, in such cases still continued to pulsate eleven times in the minute, and retained its property of responding to external stimuli. The intestinal canal, in like manner, retained its irritability; application of stimuli giving rise to contractions which were sometimes of a local nature, at other times extended for a considerable distance on either side of the part stimulated. Digestion, in like manner, suffers but little from destruction of the central parts of the nervous system; healthy frogs, and others, which had been operated upon, were, after being starved for a considerable time, fed with worms, and kept in separate glasses. In the one, as well as in the other, the worms were found after twenty-four hours to be fully digested, and the stomach and duodenum were filled with coloured mucus; such was observed to be the case even in animals whose spinal cord had been destroyed twenty-six days previously. The secretion of urine also continues: when in animals in which the brain or spinal cord had been removed, the bladder was emptied by external pressure upon the walls of the abdomen, in a short time it again became filled and distended to an enormous size, unless emptied in the way just mentioned. It had been observed by Valentin and Stilling that after destruction of the spinal cord in the frog, different derangements in the nutritive processes ensued; there were frequently observed dropsical swellings, especially of the limbs. On these also, sores formed, which often penetrated as far as the bones. In reference to these results, Volkmann states that they are, as shown by Bidder, chiefly accidental. Bidder found that when the bottom of the vessels in which the frogs were kept was covered, not with water, but with moist grass or moss, no such degenerations ensued. The rapid death which ensues in warm-blooded animals, when operated upon in the above manner, depends, according to Volkmann, upon the difficulty of sufficiently keeping up the respiration by artificial means, as well as upon the loss of blood and diminution of animal heat. The circumstance, then, that a certain number of the vital phenomena disappear suddenly and irrevocably after destruction of the spinal cord and brain, while others continue for a greater or shorter time, and this very perfectly, can only depend, according to Volkmann, upon the circumstance that the brain and spinal cord is a necessary condition for the existence of the former, but not for that of the latter. If the latter depend upon certain nervous organs, and if the nerves of the vegetative organs do not require, as a fundamental condition of their activity, the presence of the brain and spinal cord, the only possible centres on which they can depend for this are the ganglia of the sympathetic. The sympathetic and its ganglia, then, constitute, according to Volkmann, an independent whole, from which proceed the impulses to as well as the regulation of those actions which continue after the brain and spinal cord have been destroyed, and which notwithstanding require the co-operation of a central organ. That the movements in question require such an organ, and are not produced by the mere stimulus of the blood, fæces, air, &c., in the same way as the twitchings of the muscles in a frog's leg are produced by galvanism, is shown, according to Volkmann, by the different characters exhibited by the two. When stimulus acts immediately on motor nerve fibres, contraction ensues only in that muscle or part of the muscle to which these are distributed; when it affects the whole trunk of such a nerve, many muscles are excited to contraction; the contraction so produced, however, is a mere quivering, quite different from the combined and plan-like movements of the muscles of respiration, &c., or those reflex movements which are produced artificially. In these, there is a certain unity and plan, in the others not; the difference depending on the circumstance that in the one a regulating principle associates the muscular movements for the attainment of an organic object or purpose; in the others this does not take place. When the regular and plan-like manner in which the pulsations of a heart removed from the body take place, is compared with the tumultuous and purposeless quiverings of a diaphragm similarly circumstanced, it is hardly possible to suppose that the two kinds of movement proceed from the same principle. Irritability acted on by the stimulus of the blood, or air, might explain the mere contraction of the heart; the regular order, however, in which this takes place, implies the existence of a regulating principle; and a regulating principle implies the existence of a regulating apparatus. While the regular movements of the voluntary muscles suddenly cease when the brain and spinal cord are destroyed, those of the organic muscles continue; and hence their regulating apparatus cannot lie in the brain and spinal cord, and can only, therefore, be situated in the ganglia of the sympathetic.

The heart, according to Volkmann, is more flabby after death than it is during life: the intestines, in like manner, are collapsed in the dead body, and appear like so many flattened bands; while in the living body, at least in small animals, they present more the aspect of tubes; the looseness of the skin and of the scrotum in the dead body is also remarkable, compared with the appearance they present in the living. These differences depend upon a loss of tone. The tone of the involuntary or organic contractile structures does not, however, depend on the brain or spinal cord, inasmuch as it does not cease after these parts have been destroyed, but may continue in the amphibia at least for months thereafter. It depends, according to Volkmann, upon the sympathetic; and from this he derives another argument in favour of the view that the activity of the sympathetic or ganglionic nerve-fibres does not depend upon the brain or spinal cord. After division of a motor nerve, the muscles immediately became relaxed, which shows, according to him, 1st, that the tone depends on an active contraction of the muscle; 2nd, that the mere irritability of the muscle is not alone sufficient for the restoration of this contraction, but also requires an exciting cause or motor impulse; 3rd, that the nerve conveys this motor impulse to the muscle; 4th, that the place where this motor impulse arises or originates is not the nerve itself, but is a central organ. If now, after destruction of the brain and spinal cord, the tone in the organic muscles and many other contractile tissues continues, it follows from this that, besides the brain and spinal cord there must still be another centre from which motor impulses proceed, and this can only be the ganglia of the sympathetic.

In regard to this question, so far as our knowledge of the anatomical constitution of the sympathetic extends, the most probable view would seem to be that it is partly independent, in its action, of the brain and spinal cord, partly dependent. The circumstance that there are present in its branches numerous nerve-fibres which are derived from the brain and spinal cord, would appear to indicate that the organs to which such fibres proceed must be to a certain extent influenced by the central masses of the nervous system. From the circumstance, however, that it probably contains other nerve-fibres which do not arise in the brain and spinal cord, and more particularly from the circumstance of gray nervous matter being present in different parts of its extent, it seems not unreasonable to suppose that the influence which it exercises over the parts to which it is distributed originates, partly at least, not in the brain or spinal cord, but in the gray or ganglionic matter mentioned. If we attribute to the gray matter of the brain or spinal cord a certain property of originating nervous force, it seems unreasonable to deny similar properties to the gray matter occurring in other parts of the nervous system. Whatever properties are possessed by the one, analogous properties are, it is to be expected, possessed by the other. Besides, no other hypothesis which has been proposed to account for the function of the ganglia appears to harmonise so closely with known facts as that which regards them as so many distinct peripherical nervous masses endowed with properties similar to those which are commonly attributed to a nervous centre.

Properties of fibres of sympathetic. Sensory properties.— In regard to the sensory properties of the sympathetic, different statements are made by authors. Bichat, Magendie, Dupuy,* and others, observed that section of the branches of the sympathetic was attended with few or no signs of pain. Dupuy states that he has removed the superior cervical from the horse without the operation appearing to call forth any marked expression of pain. Section of the sympathetic cord in the neck may often be performed in the rabbit without any indication of sensibility being given. Haller found, on the other hand, that irritation of the hepatic plexus in the dog gave rise to distinct signs of pain: the same results were also obtained by Meyer from irritation of the solar plexus. When he made incisions into the superior cervical ganglion, he found, contrary to what had been observed by Dupuy,

* See Longet. op. cit. tom. ii.

that clear indications of pain were elicited. From ligature applied to the renal nerves, as well as from the application of chemical or mechanical stimuli to the semilunar ganglia, animals suffered great pain. So, also, Flourens* found that on irritating the semilunar ganglion in dogs the animals exhibited distinct signs of pain, and the same results were obtained by Brachet †, from irritation of the thoracic ganglia. Frequently, according to Brachet, stimuli, when first applied to a part of the nerve, do not give rise to pain; afterwards, however, when the part has been exposed to the air for some minutes, if irritation be now applied distinct signs of pain are elicited. Longet ‡, in like manner, found that on irritation of the semilunar ganglia the animal almost invariably exhibited indications of more or less pain being produced. In other animals, where the lumbar ganglia were subjected to experiment, he found, like Brachet, that it was only after prolonged irritation that signs of pain were evinced. So, also, according to Valentin §, when the cavities of the thorax or abdomen are opened as quickly as possible, and pressure applied to the semilunar ganglion, to the splanchnics, or to any other branch of the sympathetic, sometimes no signs indicative of sensibility are evinced. When, however, they have been exposed to the air for a short time they generally exhibit these properties in greater or less degree. The severe pain which frequently attends *diseases* of parts supplied exclusively by the sympathetic nerve, also affords still better evidence than can be derived from experiments of the existence of sensory nerve fibres in the sympathetic.

Different parts of the nerve appear to exhibit the property of sensibility in different degrees. In regard to this point, Valentin ‖ gives the following as the results of his experiments. 1st. The very grey branches which have passed through several ganglia do not, when the stimulus applied to them is slight, give rise to any signs which would indicate that pain was produced. Such branches are those which pass along the mesentery to the intestine; strong stimuli, however, such as the application of a ligature or of chemical irritants, cause, when applied even to these branches, distinct signs of pain. 2nd. Irritation of the ganglia themselves is followed by signs of pain either immediately or after a short time. 3rd. The connecting cord of the sympathetic is similarly circumstanced in regard to sensibility as the ganglia. 4th. The rami communicantes are as highly endowed with sensibility as the posterior roots of the neighbouring spinal nerves. He found that section

* Rech. Experimental. sur les propr. et les Fonctions du System. Nerv. p. 229., as quoted by Longet.

† Rech. Experiment. sur les Fonct. du Système Nerv. Gangl. 2nd edit., Paris, 1837, p. 357., as quoted by Longet.

‡ Op. cit. ii. p. 566.

§ Lehrbuch der Physiologie des Menschen, 1844, band ii. p. 421.

‖ Op. cit. band ii. p. 422., as quoted by Longet.

of a communicating branch did not destroy the sensibility of the corresponding ganglion: the main cord of the sympathetic must also be divided above and below the ganglion before this ensues. In the lumbar region Brachet* found that, when the communicating branches of three successive ganglia were divided, the central ganglion was deprived of its sensory properties. The greater the number of ganglia intervening between the point of the branches of the sympathetic, to which the irritant is applied, and the cerebro-spinal centres, the less distinctly, according to Valentin, does it give rise to signs of pain. Hence, the peripheral branches are the least sensitive, while the rami communicantes are the most highly endowed with this property, the connecting or main cord of the sympathetic and ganglia being intermediate in this respect between these two. The nature of the stimulus applied has also an influence on the results produced: when the ganglia are merely pricked, or their branches quickly divided, sometimes no sign of sensibility is evinced, whereas pressure, application of nitric acid or potash to the same parts give rise to distinct expressions of pain.

In regard to the experiments which are made with a view to ascertain the sensory properties of this nerve, it is to be observed that in general it is only by application of very powerful stimuli that the phenomena of sensibility are elicited: they seem to act by producing a more or less abnormal condition in the part of the nerve to which they are applied, and hence the effects they produce may be regarded as belonging to the same category as the phenomena observed in diseased conditions of the organs supplied by this nerve. In the normal or healthy condition the fibres of the sympathetic seem to be almost entirely destitute of the property of communicating impressions to the sensorium. We do not know, as Volkmann observes, whether the organic muscles be at rest or in motion; whether the glands secrete in larger or in smaller quantity; whether the gall-bladder be full or empty. We are sensible of the impressions made by the particles of food so long as they remain in the mouth, but, as soon as they reach the stomach or intestinal canal, we are no longer aware of their presence.

Motor properties.—That the sympathetic contains motor nerve fibres there can be no doubt; irritation of its branches being followed by movements in the different muscular organs to which they are distributed. Thus irritation of the splanchnic nerves in the living animal, or immediately after death, is generally followed by more or less extensive contractions in the small intestine. Müller observed that the same result followed irritation of the semilunar ganglion: the same observation has also been made by Kürschner.† Mechanical or chemical irritation, but especially galvanic

* Op. cit. p. 360., as quoted by Longet.

† Abhandlungen über das Nerven System, von M. Hall. Aus dem Englischen von D. C. Kürshner, Marburg, 1840, Nachtraege, p. 182.

stimulus applied to the filaments of the sympathetic which pass to the heart, have the effect of accelerating the pulsations of that organ and of exciting it to renewed contraction after it has ceased beating. As movements very frequently arise in organs supplied by the sympathetic, especially in the intestines, spontaneously, at least under the stimulus of the atmospheric air, it is sometimes difficult to determine whether the contractions which follow the application of a stimulus to any of the nerves be really caused by this, or whether they may not belong to those just mentioned. Frequently, however, the contraction follows the irritation so regularly as to leave no doubt that the two are connected; if, moreover, the abdominal muscles in the cat or rabbit be removed, so that the thin and transparent peritoneum alone remains over the viscera, application of mechanical or chemical irritants to the splanchnic nerves in the thorax may still be observed to be followed, in many cases at least, by contractions in the intestine. In such experiments the air is prevented from acting upon the viscera by the intervening peritoneum, and in this way the fallacy above mentioned is less liable to occur.

It remains to consider the motor influence of the sympathetic in reference to the different muscular organs supplied by it.

Heart.— The heart, as has been already stated, derives its nerves from the sympathetic and pneumogastric. That the branches which are supplied by the sympathetic exercise an influence over the movements of the heart, is shown by what has been already stated, that after it has ceased to beat, irritation of the branches which pass to it from the cervical ganglia will again excite it to contraction. Similar results frequently follow irritation of the ganglia themselves. When the galvanic stimulus is applied to the cardiac branches of an animal in which the heart has not yet ceased pulsating, the effect is to augment the number of beats, and at the same time to increase their strength. In a rabbit in which the heart's action had ceased, Valentin * found that when the wires of the magneto-electric apparatus were applied, about $\frac{1}{4}$ of a millimetre distant from each other, upon the second thoracic ganglion of the right side, a very powerful contraction in the auricles immediately ensued: the experiment was repeated several times, and with the same result. This also took place when the same stimulus was applied to the first thoracic ganglion. When, on the other hand, the wires were laid upon the aorta at the distance of $\frac{1}{4}$th of a millimetre from the heart, or upon the surface of the right ventricle, no effect was produced. He concludes, therefore, that the stimulus when applied to the nerves was, in this case, more effectual than when applied to the muscular fibres themselves. As regards the function of those filaments which are sent by the pneumogastric to the heart, E. H. Weber † believes that they exercise a restraining influence over the movements of the organ; stimulus applied to the pneumogastric, according to his experiments, having the effect of retarding or altogether stopping its movements. When the stimulus of the electro-magnetic rotation apparatus was applied to the bulbus arteriosus in the frog's heart,—the part of the organ around which the fibres derived from the sympathetic are, according to him, chiefly distributed,—he found that the pulsations were increased in number as well as in strength. When, on the other hand, the same stimulus was applied to the upper portion of the inferior vena cava, where the filaments of the pneumogastric are mainly distributed, the effect produced was not an acceleration but a retardation or stoppage of the heart's action. When a defined part of the vagus has been stimulated for some time continuously, the heart again begins to pulsate: when a portion of the nerve above this point is now stimulated, no effect is produced; when, on the other hand, the stimulus is applied to a portion further down, nearer the heart, a cessation of its movements is again produced. The circumstance that the heart, after the stimulus has been applied to the pneumogastric for some time, again commences to beat, is attributed by Weber to the part of the nerve becoming exhausted, or losing its restraining influence, when the heart, being thus freed again, begins to pulsate. Budge*, however, attributes the cessation of the movements of the heart, produced by the application of galvanic stimulus to the pneumogastric, not to any restraining power exercised by that nerve, but rather to a temporary exhaustion produced by the strength of the stimulus. In support of this view, he states that, although the movements of the iris chiefly depend upon the oculo-motor nerve, yet Weber found, when the wires of the magneto-electric rotation apparatus were applied to this nerve within the cranium, that the pupil became dilated, remaining so for a considerable time after stimulus had been withdrawn, and then again slowly contracting. The effects thus produced upon the iris are, according to him, analogous to those produced upon the heart by application of the galvanic stimulus to the pneumogastric. Moreover, the nerves which are sent to the heart of the frog do not present the arrangement which Weber has described. No other filaments than those which pass from the vagus are distributed to the heart of this animal, at least no others have been demonstrated. The vagus nerve becomes united with the sympathetic in the ganglion, which is situated about one line from the root of the pneumogastric; and from this ganglion, which contains fibres of the vagus and sympathetic, springs, amongst other branches, a slender filament which is destined for the heart. This runs downwards on the inner aspect of the lungs, and passes along the veins to the auricles and ventricle, the former receiving the greater number of the nerve fibres. The branch in

* Loc. cit. p. 427.

† Wagner's Handwörterbuch der Physiologie, band iii., Abtheilung ii. p. 45.

* Wagner's Handwörterbuch, band iii. p. 415.

question contains fibres derived both from the sympathetic and also from the pneumogastric. Again, such a restraining power must hold an opposite relation to the moving power in the normal condition ; the moving power would therefore express itself only in part, according as the other is in a latent state or in a state of activity, and consequently section of the vagus nerve ought, did it exert the restraining power in question, to be followed by an acceleration in the movements of the organ, which is not the case. Budge, therefore, seems to regard the fibres which are sent to the heart in the frog by the pneumogastric, as possessed of motor and sensory properties.

Schiff also found that when the heart's action has been made to cease by application of the wires to the groove between the auricles and ventricles, this effect cannot be counteracted by applying them to the bulbus arteriosus. The phenomenon of the cessation of the heart's action, produced by the application of the galvanic stimulus to the pneumogastric, he explains by supposing that its fibres are in a state of activity during the systole of the corresponding part of the heart, but quickly become exhausted, thus allowing the diastole to take place: thereafter, their activity being again renewed, a second systole results. When therefore, strong galvanic stimuli are applied to the nerve the state of exhaustion continues longer and in the same proportion the diastole, or cessation of the heart's action, is also longer.

In accordance with the above views, Valentin * in like manner holds that the sympathetic has no influence over the movements of the heart in the frog, neither giving rise to acceleration nor stoppage of its action.

In regard to the connection between the central masses of the nervous system and the action of the heart, it is evident, from what has been above stated in regard to the effects which are produced by the application of the galvanic stimulus to the pneumogastric nerve, that a certain influence must be exercised by these. By Willis †, and others, it was held that the movements of the heart, as well as of the other inorganic muscles, depend upon the cerebellum. This they believed from the circumstance that the nerves which preside over the involuntary actions were supposed to take their origin from this part of the nervous system, and also from observing that wounds upon the back part of the head proved speedily fatal. Haller ‡, again, endeavoured to show that the action of the heart is entirely independent of nervous influence, and is due merely to the inherent irritability of the muscular fibres. From the circumstance that sudden destruction of the spinal cord immediately produces an interruption of the heart's action, Legallois concluded that its movements are not due to inherent irritability, as Haller maintained, but depend upon the spinal cord. The cessation produced in the way just stated, although indicating that an influence may be exercised through the central nervous masses upon the movements of the heart, by no means implies the conclusion which was drawn from it by Legallois, inasmuch as the heart may sometimes in such cases again begin to pulsate. That the heart may be influenced in its action through the medium of the central masses of the nervous system is also shown by the effects which are produced by the application of the galvanic stimulus to these parts. Thus, in the frog, as shown by the experiments of Weber *, Budge †, Valentin ‡, and others, it may be made to cease pulsating by applying the wires of the magneto-electric rotation apparatus to either side of the medulla oblongata. Unless there has been much loss of blood in exposing the parts the heart becomes dark-red, and is very much distended; where the large blood-vessels have been previously cut the heart still ceases to pulsate when the stimulus is applied as above: it does not, however, present the dark-red distended appearance, but is more or less collapsed and pale. The experiment, according to them, seldom or never fails. If the electric stimulus has been applied for too long a time the heart again begins to beat, in the same way as takes place when the stimulus is applied to the trunk of the pneumogastric nerve. The same stimulus also sometimes produces more or less change in the rhythm of the organ. According to the Webers, the portion of the central nervous masses which, when stimulated in this manner, gives rise to a cessation in the action of the heart, is that extending from the corpora quadrigemina to the posterior extremity of the calamus scriptorius. Budge found, in his experiments, that the corpora quadrigemina were not so intimately concerned in the production of these effects as the medulla oblongata. Tiedemann § appears to regard the cerebellum and the medulla oblongata as the parts through which the cessation of the heart's action may be induced, while stimulus applied to the corpora quadrigemina produces no effect. Valentin believes that while the corpora quadrigemina and cerebellum exercise a certain influence, the medulla oblongata is the part chiefly concerned. In nine mice, which were rendered insensible by chloroform, and whose hearts and medulla oblongata were laid bare, Valentin endeavoured to ascertain the parts of the central nervous masses which, when stimulated in the way above mentioned, give rise to cessation of the heart's action, as also the effects which are produced by the same stimulus when applied to the spinal cord. In none of them did he observe any

* Loc. cit. p. 694.

† Cerebr. Anatomia Nervorumque Descript. et Usus, p. 195.

‡ Dissertat. sur l'Irritabilité, t. i. p. 72.

* Weber, Wagner's Handwörterbuch, band iii., 2nd Abtheil, p. 44.

† Ibid. p. 415. &c.

‡ Lehrbuch der Physiologie, band ii. p. 464., et seq.

§ Müller's Archiv. 1847, p. 498.

stoppage of the heart's action when the cerebellum, or corpora quadrigemina were the parts to which the stimulus was applied: when applied to the medulla oblongata, on the other hand, this effect was invariably produced. The cervical part of the spinal cord, when stimulated, gave different results. In a mouse, which had been under the influence of the narcotic for 2½ minutes, the heart was repeatedly made to cease pulsating when the wires were applied upon either side of the spinal cord in the region of the third to the fourth cervical vertebra, and also when applied to the part between the first and second cervical vertebræ. After repeating this experiment several times, and with the same result, he cut the spinal cord across in the region of the second to the third vertebra; when the stimulus was now applied to the lower cut extremity of the cord the heart's action was accelerated. The cessation produced by application of the stimulus to this part of the spinal cord in the former experiment was, therefore, according to Valentin, probably due to its being transferred along the spinal cord to the medulla oblongata. In two other animals it was found that the two lower thirds of the cervical portion of the cord in like manner gave rise to no cessation in the heart's action, but rather, after the first few seconds, caused it to be accelerated. A young rabbit was strangled, the head separated from the body at the articulation between the occipital and first cervical vertebræ, and artificial respiration kept up. When the wires of the battery, moderately loaded, were now applied to the upper part of the spinal cord, in the region of the first cervical vertebra, the heart, which was before at rest, commenced pulsating. The spinal cord was laid bare from the first cervical to the eighth thoracic vertebra. When the wires were inserted in the region of the fifth cervical to the second thoracic vertebra, the heart's action was distinctly accelerated. When the spinal cord was removed, the same result still followed upon application of the wires, because the roots of the nerves were stimulated. When the heart was cut out of the body, and again placed *in situ*, the above experiment was repeated without effect.

Just as stimulus of the sympathetic branches in the mammalia is followed by acceleration of the heart's action, while stimulus of the pneumogastric causes it to cease pulsating, so also Valentin concludes, from the above experiments, that stimulus applied to the spinal cord gives rise to the former result, while from stimulus applied to the medulla oblongata the latter result ensues. In the frog, according to Valentin, the spinal cord has no influence over the movements of the heart. He also holds, as already stated, that in this animal, the sympathetic, in like manner, exercises no influence in this respect.

In a pigeon, he found that when the wires of the magneto-electric apparatus were inserted into the cerebellum, the heart's action became more or less laborious: when applied to the spinal cord, in the region of the first cervical vertebra, forwards, towards the medulla oblongata, the heart's action was repeatedly brought to a stand.

The cessation in the heart's action by application of the galvanic stimulus to the medulla oblongata most readily ensues, according to Valentin, when the wires are applied to its sides, or to the under surface in the vicinity of the roots of the eighth pair, and in no instance does it ensue when the wires are applied to any part of the central nervous masses after removal of the medulla oblongata.

The influence exercised upon the heart's action by the central nervous masses is also shown by the diminution in the number as well as in the strength of its pulsations, which ensues when these are removed, especially on removal of the medulla oblongata. That the diminution in question does not depend entirely upon the stoppage of the respiratory process consequent on the destruction of the medulla oblongata, has been shown by Budge. When, in the frog, the anterior portion of the medulla is left, the lungs continue to act; and yet, according to him, the pulsations of the heart diminish very rapidly both in strength and in frequency. He finds that, although removal of the other parts of the central nervous masses produces little immediate effect on the heart's action, it seldom continues for any length of time after the removal of the medulla oblongata. The effects which follow disease of these parts in like manner illustrate the influence which they exercise over the movements of the heart. In compression of the brain, as well as from lesion of the upper part of the spinal cord, the pulsations are frequently diminished: the effects of shock in altogether stopping its action also illustrate the same thing.

From the experiments above mentioned, Valentin and others hold that the nervous centre upon which the heart's action depends is the medulla oblongata. The particular rhythmical order in which its different parts contract is due, according to some, to peculiarities in the manner in which they are acted upon by the blood, the contact of arterial with the lining membrane of the left cavities of the organ, that of venous blood with the lining membrane of those of the opposite side, furnishing the proper stimuli, in obedience to which these parts contract. The successive contraction of auricles and ventricles is in like manner explained by the blood first entering the former, and causing them to contract. By their contraction it is propelled into the ventricles, and stimulates these to contraction also, while the contraction of the ventricles causes the auricles to become again filled with blood from the veins, and so on indefinitely. This rhythmical order in the movements of the organ has also been attributed to peculiarities in the mode of arrangement of its muscular fibres. The muscular fibres of which it is composed, as may be seen on examining with the microscope the auricles in the heart of the frog or other small animal, do not lie parallel to one another, as in the ordinary muscles, but cross one another in different directions, many of the bundles being at the same time observed to present a more or less branching character. The branches or divisions of one bundle cross those of neighbouring bundles. In this manner the fibres form a number of reticulated layers laid over one another, while at the same time bundles pass from one layer into the adjacent layers, so that a more or less complete intermixture of the fibres takes place. The fibres composing the ventricles also present more or less of this reticulate arrangement. Moreover, many of the fibres of the auricles pass into those of the ventricle, and *vice versâ*. In virtue of such an arrangement of the fibres, stimulus applied to one part of the heart gives rise to a contraction in the bundle to which it is applied: since this crosses neighbouring bundles its contraction acts as a stimulus to these, in obedience to which they also contract. In this manner, the contraction is not limited to the fibre, or bundle of fibres, to which the stimulus is first applied, but extends over the entire mass. So also the contraction of the fibres, which are described as passing between the auricles and ventricles, stimulate the fibres of which the latter are composed, giving rise to a general contraction in them also; and in this way the successive contraction of auricles and ventricles is produced. According to Schiff, as mentioned by Valentin, the movements of the heart may be reduced to the peristaltic or vermicular type. He holds that in a certain part of the muscular substance are contained the nerves which preside over the movements of neighbouring bundles. When this contracts, a stimulus is thereby given to the nerves which supply the portion of the muscular substance immediately succeeding; so that in this manner a number of progressive contractions of the successive bundles of fibres are produced. The contraction of the auricles or ventricles is thus not a single simultaneous act; but is made up of a great number of contractions succeeding one another, in the same manner as is seen in the contraction of the intestine. It is the rapidity with which they follow one another that gives rise to the appearance of their being simultaneous. These contractions travel from auricle to ventricle, giving rise to the successive contractions of these parts. He finds that when a ring of the muscular substance at the base of the ventricle in the frog's heart is brought, by local application of the galvanic stimulus, into a state of continued or spasmodic contraction, the due rhythm between the contraction of the auricles and the part of the ventricle below the contracted portion ceases. When a spasmodic contraction is produced in a part of the ventricle by external stimulus this part may be irritated without giving rise to any general contraction. He also finds that when a portion of the ventricle of a heart which still retains its irritability, is stimulated, the contraction is sometimes seen to take place in this before it takes place in the other portions; the stimulated portion is also the part which first becomes relaxed in the diastole of the organ.

In opposition to the view above mentioned Volkmann* maintains that the movements of the heart cannot depend upon the central nervous masses. It continues its pulsations after the brain and spinal cord have been removed. When, however, the rhythmical movements of a part depend upon a nervous centre, they cease immediately after the connection between these parts and the nervous centre is broken. The rhythmical movements of the muscles of respiration depend upon a nervous centre, the medulla oblongata. So soon as this is destroyed they cease. In like manner the heart, were the medulla oblongata, or any other part of the central masses of the nervous system the centre upon which its movements depend, must also cease pulsating so soon as it is removed from the influence of these. According to the experiments of Bidder, however, already mentioned, frogs may live for six weeks after the spinal cord has been destroyed, the circulation, as seen in the web of the foot, going on as livelily as before, and presenting no difference when compared with that in the healthy animal. So also when the entire central masses of the nervous system are removed the heart still continues its pulsations until the second day. The movements exhibited by the heart, after the central masses of the nervous system have been destroyed, cannot, according to Volkmann, be explained as mere movements of irritation, due to the inherent irritability of the muscular fibres, acted on by the stimulus of the blood or of the atmospheric air. Mere irritability, acted on by the stimulus of the blood, or of the air, cannot explain why both auricles or both ventricles should contract at one and the same time; and just as little can we in this way explain the successive contraction of auricles and ventricles. To explain the rhythmical order in which these contractions take place it is necessary to suppose that they, like movements of a similar kind, such as those of the respiratory muscles, are regulated by a nervous centre. The fact that the heart's movements continue after it has been removed from the body indicates, moreover, that the centre upon which its movements depend must be contained in the organ itself. It has been already mentioned that in different parts of the heart are found small ganglia. These are believed by Volkmann to be the centres on which its movements depend. These, according to him, act as organs from which the impulse to contraction proceeds: they are also so connected with one another as to act in concert, the impulses proceeding in such directions as to give rise to the regular succession in which the contractions of the different parts take place.

The effects produced upon the heart's action by stimuli applied to the central masses of the nervous system, and upon which the

* Loc. cit. p. 616. &c.

view that its movements depend upon these parts is chiefly founded, are explained by Volkmann as taking place by reflex action through the medium of the sympathetic ganglia. The fibres which pass from the spinal cord to the ganglia stand to the proper sympathetic fibres arising in these in the same relation in which the ordinary sensory fibres stand to the motor fibres of the muscles of animal life.

A conclusive way of determining whether the movements of the heart, as well as the order in which these take place, depend, or not, upon the ganglia contained in its substance, would be to ascertain whether they still continue after the ganglia have been extirpated. These, however, are so small, and apparently so numerous, as to render such an experiment impossible. That the continuance of these movements after the brain and spinal cord is destroyed, as well as when the heart is removed from the body, cannot be attributed to mere irritability of the muscular fibres acted on by the stimulus of the blood or of the atmospheric air, but must be connected with nervous influence, is rendered probable by several circumstances, but especially by the observation first made by Henry, and afterwards by Müller *, that solution of opium or of other narcotic substances, when applied to the outer surface of the heart, does not produce any obvious alteration in its action, whereas when introduced into its cavities so as to be brought into contact with its inner surface, their almost immediate effect is to cause this to cease. Again, when stimulus is applied to one of the ventricles of a heart which has just ceased pulsating, the contraction thereby produced does not commence at the point irritated, as might be expected were the irritability of the muscular fibres alone concerned, but in the auricles, and is followed by contraction of the ventricles. Sometimes, indeed, stimulus applied to the ventricles is followed by contraction of the auricles alone. Even when the stimulus is applied to the apex of the organ, the contraction still commences in the auricles, and sometimes limits itself to these. The regular order in which its movements take place, so different from those produced in the ordinary muscles by direct application of external stimuli, would imply that the impulse by which they are produced must be conveyed in a certain definite direction to the different muscular parts of which the heart is composed; and this can only be supposed to be effected through the medium of its nerves. The mere arrangement of the muscular fibres of the heart seems insufficient to account either for the general contraction of auricles and ventricles or for the order in which these succeed one another. If, in the case of the heart, the contraction of a single bundle of the muscular fibres may act as a stimulus to the neighbouring fibres, by which they also are excited to contraction, the same thing ought to take place in the muscles of animal life: the bundles in these, though presenting a different arrangement from those in the heart, are, notwithstanding, in as close contact with one another as are the latter, and have equal facility for stimulating the neighbouring bundles to contraction. The dependence of the rhythmical movements of the heart upon a certain arrangement of its nerves, and moreover that there are certain portions of the same from which the stimuli to contraction proceed, is further indicated by the effects, as shown by Volkmann, which follow incisions made into the heart's substance. When a transverse incision is made through the heart, between its auricles and ventricles, the former have been found to continue their contractions much longer than the latter; and if a longitudinal incision be made gradually proceeding from apex to base, the rhythm is preserved in both portions until the heart has been divided half way; when the incision is continued further, however, the movements of either part become irregular. When the ventricle is divided transversely into two portions, that towards the apex either ceases its contractions immediately or continues the same only for a short time, whereas that which is still in connection with the auricles goes on contracting as before.

It has also been observed that in the heart of the frog there is one portion of the septum between the auricles which continues its contractions much longer than any other part; and in this portion the greatest number of the cardiac ganglia and nerves are situated. It was also observed by Kölliker that the transverse groove in the frog's heart in like manner exercised a marked influence on its rhythmical contractions; and here also the ganglionic corpuscles and nerves are very abundant. In young kittens and rabbits also, Valentin has likewise observed that the groove in question affects the movements of the heart very much.

The opinion of Volkmann, therefore, that the rhythmic contractions of the heart are connected with a nervous centre, and moreover that this nervous centre is the sympathetic ganglia contained in the heart's substance, seems highly probable. At the same time there cannot be the least doubt that an influence may be exercised over these movements by the central masses of the nervous system.

Intestinal canal. Œsophagus. — The œsophagus receives nerve-fibres both from the pneumogastric and sympathetic. The former is, according to Longet *, the source of its sensibility as well as of its motion, while the sympathetic presides over the secretion of the mucus with which its inner surface is lubricated. Valentin, however, as mentioned by Longet, found, on irritating the cervical portion of the main cord of the sympathetic in the rabbit, that movements were produced in the middle portion of the œsophagus; and contractions were also produced in the thoracic portion of the same tube when the inferior cervical ganglion or either of the first four thoracic ganglia was irritated.

* Müller's Archiv. 1845, p. 423, et seq.

* Op. cit. p. 607.

Longet, on repeating the experiments of Valentin, failed to observe any contractions, and concludes that Valentin must have irritated the pneumogastric as well as the sympathetic. It is only (according to Longet) when the pneumogastric or spinal nerves are irritated, that such contractions ensue; and, moreover, section of the eighth pair is attended by complete paralysis of the œsophagus.

Stomach.—The stomach, like the œsophagus, is supplied by branches of the pneumogastric and sympathetic. Irritation of the former is almost always followed by contractions in this organ. Irritation of the splanchnic nerves, or of the semilunar ganglion, according to Longet *, produces no such effect. Valentin, on the other hand, found that stimulus applied to the main cord of the sympathetic in the neck, or to the inferior thoracic ganglia, in the rabbit, gives rise to contractions in this organ. Volkmann † has also found that when the stimulus of the electro-magnetic rotation apparatus is applied to the thoracic portion of the sympathetic in the cat it gives rise to powerful peristaltic movements in the stomach. He also observed still more lively contractions excited in the stomach of a young dog when the same stimulus as in the previous experiment was applied to the sympathetic cord in the thorax, or to the greater or smaller splanchnic nerves before they enter the semilunar ganglion. It would seem, therefore, that, besides the motor filaments which are sent to the stomach by the pneumogastric, it also receives others through the medium of the sympathetic.

As regards the movements of the small intestine, &c., it is almost invariably excited to contraction by irritation of the splanchnic nerves or semilunar ganglion. After the movements produced in the intestine by the stimulus of the air, acting upon them when the cavity of the abdomen is laid open, have subsided, contractions extending over the greater part of the gut may still be produced, as was first shown by Müller, by application of chemical irritants, such as potash, to the solar plexus. According to Valentin, the movements produced by irritation of the splanchnic nerves are chiefly confined to the duodenum and upper part of the jejunum, while irritation of the solar plexus, on the other hand, is followed by contractions which extend over the whole of the small intestine. Irritation of the sympathetic cord in the thorax as high up as the fifth or sixth ganglion, and also in the lumbar region, gives rise, according to Valentin, to distinct contractions in the small intestine, while stimulus applied to the lumbar and sacral portions acts very energetically upon the great intestine and rectum. The influence of the sympathetic over the movements of the intestines is also shown by the observation of Valentin that when the branches which pass along the mesentery are irritated, contractions are produced in the particular portions of the intestine to which they are distributed, while the rest of the gut remains quite motionless.

* Op. cit. p. 609.

† Müller's Archiv. 1845, p. 414., &c.

Budge observed that movements were excited in the cœcum of the rabbit when the trunk of the vagus-nerve in the neck was stimulated by means of the electro-magnetic rotation apparatus.

As in the case of the heart, so also in regard to the intestinal canal, stimuli applied to the central nervous masses have been observed to exercise a greater or less influence in exciting contractions in the intestine. In animals newly killed, Valentin has frequently observed movements produced in the intestines by division of the anterior and posterior roots of the spinal nerves. In such experiments, however, it is difficult to ascertain whether the contraction be due to the stimulus applied to the nerves, or whether it may not be owing to the stimulus of the air acting directly on the intestines themselves. The application of galvanic stimulus leads to more decisive results. When, according to Valentin*, the wires of the magneto-electric apparatus are applied to the corpora quadrigemina or medulla oblongata, lively contractions are excited in the stomach and intestine. Contractions were also produced in the small intestine, great intestine, and rectum, by application of the same stimulus to the spinal cord. In *Cyprinus tinca*, Weber has shown that very powerful contractions may be excited in the stomach by application of the wires of the electro-magnetic rotation apparatus to the posterior part of the cerebellum or to the medulla oblongata. The same stimulus applied to the spinal cord in the animal above mentioned, as also in dogs, he observed to be followed by movements in the intestinal canal.

From the experiments of Valentin it appears that the movements which are excited in the intestinal canal by stimulus applied to the central masses of the nervous system, are not produced through the medium of the pneumogastric alone. In a rabbit which had been bled to death, and in which the abdominal muscles were removed without injuring the peritoneum, he found, when the wires of the magneto-electric apparatus were inserted into the cerebellum, that very lively movements ensued in the small intestine, although the two vagi nerves had been previously divided in the neck. Budge, however, finds that it is only when the two vagi nerves have been left that movements can be excited in the cœcum of the rabbit by application of the galvanic stimulus to the medulla oblongata.

The constipation and tympanitis which frequently attend diseases of the spinal cord, in like manner indicate that the central masses of the nervous system exercise a certain influence over the movements of the intestinal canal.

These movements, however, like those of the heart, still continue after the brain and spinal cord have been destroyed. Bidder, as

* Op. cit. p. 466., &c.

cited by Volkmann, fed several frogs with worms and immediately destroyed the spinal cord: on opening the animal twenty-four hours afterwards, the stomach was found distended with tough slimy matters: if, on the other hand, forty-eight hours were allowed to elapse before the stomach was examined, it was found almost empty, part of the contents having been probably absorbed, while part had passed downwards into the intestinal canal. The continuance of the movements of the intestinal canal after the brain and spinal cord have been removed, would seem to indicate that these are not the immediate centres on which their contractions depend. The contractions which take place may be explained as due to the inherent irritability of the muscular fibres, while their type may be said to be owing to a peculiar arrangement of these, by which the contraction of one bundle acts as a stimulus to the neighbouring bundles, exciting these to contraction also, and in this way giving rise to the vermicular movements of the gut. It seems probable, however, that they are regulated by the ganglia of the sympathetic, especially since it has been observed by Henle*, that in pieces of the intestine which have been cut away close to the line of attachment of the mesentery, the contractions produced by application of local stimuli extend but a little way on either side of the point irritated, and are comparatively feeble. When a part of the mesentery is removed along with the portion of the intestine, they are more powerful and more extended, and are most so when the intestine and mesentery are left in their normal relations.

Genito-urinary organs. — Contractions of the ureters have been frequently observed by Valentin † to follow irritation of the abdominal ganglia of the sympathetic. They present the same peristaltic character as those of the intestines, and pass downwards from the kidney towards the bladder. In the bladder contractions are more easily produced than in the ureters: sometimes shortly after opening the abdominal cavity of an animal newly killed, the bladder contracts so powerfully as to give rise to an expulsion of its contents. Contractions may be excited in it, according to Valentin, by irritation applied to the sympathetic cord in the abdomen or pelvis, or to the lower lumbar and upper sacral ganglia; the contraction commonly commencing on that side of the bladder on which the nerves have been irritated. The last lumbar and first sacral ganglia are described by him as having most influence over its movements. In the vas deferens powerful contractions have been observed by Valentin when stimulus was applied to the two last lumbar ganglia: the rabbit and guinea-pig were the animals on which this experiment was made. In the latter animal the vesiculæ seminales were also excited to contraction by irritation applied to the lower lumbar and upper sacral portions of the sympathetic, sometimes so powerful as to expel the contents through the opening of the urethra. Stimulus applied to the same parts in the female gives rise to contractions in the Fallopian tubes. The uterus may, according to the same observer, be excited to contraction by stimulus applied to the lower lumbar and upper sacral ganglia, or to the branches given off from these. The contraction in such cases passes downwards from the Fallopian tubes towards the vagina.

In regard to the influence of the central parts of the nervous system over the movements of these organs, it would appear, from Valentin's experiments, that contractions may be excited in the urinary bladder by stimulus applied to the spinal cord. The ureters are also said to exhibit contractions when the wires of the magneto-electric apparatus are brought into contact with the medulla oblongata, or with the spinal cord in the cervical or thoracic regions, as also when they are applied to the right optic thalamus. The same also holds true, according to him, regarding the vasa deferentia, Fallopian tubes, and uterus. He has further observed, that often when the stimulus is applied to one side of the central nervous masses, it is the organ on the opposite side which is excited to contraction: thus stimulus applied to the right optic thalamus not unfrequently acts on the ureter of the left side; in like manner, when the right hemisphere of the cerebellum is the part irritated the contractions sometimes take place in the Fallopian tubes or vas deferens of the left side.

These organs, however, like those already mentioned, exhibit their usual contractions after they are removed from the influence of the brain and spinal cord. The fact that in paraplegic women delivery has taken place, would appear to show that the contractions of the uterus are not dependent upon the central masses of the nervous system: this is also shown by an experiment of Segalas*, that division of the spinal cord in the lumbar region in the rabbit does not prevent the completion of the labour. Moreover, it would appear, from a series of experiments made by Professor Simpson of Edinburgh, that the whole process of labour may be completed, although the spinal cord has, in great part, been previously removed.

Pupil. — It was long ago ascertained by Pourfour du Petit †, that section of the main cord of the sympathetic in the neck is very quickly followed by contraction of the pupil, besides certain other phenomena. The same experiment has since been made by Molinelli, Dupuy, Reid, Valentin, and others.‡ Molinelli regarded the effect produced upon the pupil not as an immediate effect of the operation, but as an after result;

* Allgemeine Anatomie, p. 724.
† Op. cit. p. 468.

* Bulettin de l'Academie de Medicine, tom. ix. p. 1124.
† Histoire de l'Academie, 1727, 1729, Paris, p. 5. et seq.
‡ See Budge, in Vierordt's Archiv. für physiologische Heilkunde, 1852, Ergänzungs Heft.

by Dupuy, on the other hand, it was described as the immediate consequence of the same. Reid found in his experiments that the contraction of the pupil invariably takes place in the dog and cat, but in the rabbit the result is not so constant. Reid also showed that it was not the section of the trunk of the vagus, but that of the sympathetic, that was the cause of the contracted state of the pupil. According to Valentin the effects produced differ considerably in different animals: in the dog the pupil becomes very much contracted: the contraction is not immediate, but ensues within about half a minute after the nerve has been divided. Stimulus applied to the nerve still causes the pupil to dilate, but in a few minutes it again contracts, until it is not larger than the head of a pin, and remains so for months. The contracted pupil has generally a circular form; there are, however, occasionally seen particular inequalities in its margin which change from time to time. When belladonna is applied the contracted pupil dilates, but does not reach the size which the sound pupil attains under similar circumstances. When the aqueous humour is tapped the contracted pupil becomes slightly widened, while at the same time it assumes a longish round form. In the sound eye when treated in this way the pupil becomes diminished in size.

Biffi found that slight dilatation of the pupil followed irritation of the ascending or carotid branches of the sympathetic, division of these being also followed by contraction of the pupil, though to a less extent than takes place after division of the sympathetic cord in the neck. Irritation of the superior cervical ganglion gives rise to the greatest dilatation of the pupil; so also when the same is extirpated the contraction of the pupil is very great.

A number of researches have recently been made, in regard to this subject, by Budge* and Waller. When the stimulus of the magneto-electric apparatus is applied to any part of the sympathetic cord in the neck, dilatation of the pupil takes place; the part of the nerve nearer the chest being, however, less irritable than that higher up. The superior cervical ganglion is not only more susceptible of the stimulus than any other part of the nerve, but the effect produced upon the pupil also lasts longer. The dilatation of the pupil may be produced by the application of the galvanic stimulus to any part of the sympathetic, from the inferior cervical ganglion to the ophthalmic ganglion. Irritation of the sympathetic below the inferior cervical ganglion, however, has no effect upon the pupil. As regards the origin of the fibres in the sympathetic which influence the pupil, they might be supposed to proceed from three sources: — 1st. They might be regarded as prolonged upwards from the thoracic portion of the main cord, the inferior cervical ganglion being an organ interposed to prevent the transmission of stimuli. Against this view, however, there is the circumstance that the fibres still pass through three ganglia before they reach the eye, the superior cervical, Gasserian, and ophthalmic. 2nd. They might be supposed to arise in the inferior cervical ganglion, or to be derived from the spinal cord through the medium of the rami communicantes. If they arise in the ganglion, the section of the sympathetic cord below this, or of the branches which are connected with the ganglion, ought not to give rise to any contraction of the pupil, this depending, according to Budge, upon the separation of the nerve-fibres from their centre. In a dog which had been put under the influence of chloroform, the inferior cervical ganglion was sought, and the main cord of the sympathetic below the ganglion, as well as all the branches in communication with the latter, were divided one by one. Of all these, only one was found which acted on the pupil. Division of this branch sometimes gave rise to as decided contraction of the pupil as division of the sympathetic cord in the neck. In order to ascertain whether the branch in question has its origin in the spinal cord, the following experiment was made. A rabbit was put under the influence of ether, and the sympathetic of the left side divided in the neck; the spinal column was then opened and the spinal cord cut across in the region of the third dorsal vertebra, and galvanic stimulus applied to the upper cut extremity of the cord; straightway the pupil of the right side dilated, while that of the left side, on which the sympathetic had been cut, did not vary in the slightest. From further experiments it was found that stimulus applied to the spinal cord below the sixth dorsal vertebra has no action on the pupil; above this point, however, and as high up as the fifth cervical vertebra, dilatation was observed on application of stimulus; the portion of the spinal cord which has most influence on the pupil being that in the region of the first three thoracic vertebræ.

As regards the particular fibres in the sympathetic on which its sensory and motor endowments depend, Volkmann* believes that none of the fine fibres, described by him as sympathetic fibres, are possessed of sensory properties in their normal condition. In support of this view, he states, 1st. That the number of these fibres is greatest in parts which are least sentient, as is the case more or less with all the organs of vegetative life, and especially with the pia and dura mater, and arachnoid, with the periosteum and with the blood-vessels. The circumstance that these parts are so very seldom, and some of them never, the seat of impressions which are transmitted to the sensorium, must, Volkmann observes, raise a suspicion that the very rich network of nerve-fibres which occurs in them are not possessed of sensory properties, and the results derived from experiments, as

* See Budge, in Vierordt's Archiv. für physiologische Heilkunde, 1852, Ergänzungs Heft.

* Loc. cit. p. 601.

well as from surgical operations, would seem to show that such is the case. The coats of the blood-vessels he considers to be destitute of sensibility, inasmuch as he found that the operation of fixing the hæma-dynamometer into them gave rise to no distinct sign of pain. 2nd. As regards the fibres which take their origin from the ganglia, it seems in a high degree probable that they at least cannot convey impressions from the organs which they supply to the sensorium. In order to communicate such impressions they must transfer them to fibres which do not terminate in the ganglia, but are directly or indirectly connected with the sensorium, and are, in short, true sensory fibres. Such a transference in the normal condition does not, however, appear to take place. 3rd. It is not at all probable that fibres, which in animals that have been beheaded, or are under the influence of strychnine, show so little connection with the spinal cord that stimulus applied to them cannot excite any reflex movements in the voluntary muscles, should be in a condition to communicate impressions through the spinal cord to the sensorium. 4th. Division of the cerebro-spinal nerves which supply the integument is followed by loss of sensibility in that part, although the sympathetic fibres passing to the same have been left uninjured. In the frog, a great number of fibres are sent from the sympathetic to the cerebro-spinal nerves, and are along with these distributed in considerable quantity to the integument: if now the nerves in the leg of the frog be divided above the point at which the fibres of the sympathetic join them, so as in this way to leave the continuity of the latter uninjured, the limb is notwithstanding deprived of sensibility; the power of exciting reflex action in the muscles of the limb by stimulus applied to the integument being also at the same time destroyed. Division of the fifth nerve, in like manner, is attended by loss of sensibility in all the parts of the face supplied by this nerve; and no reflex action can be excited by stimulus applied to the eye, tongue, &c., although these parts derive fibres from the sympathetic, which are not divided in the operation. Although in the normal condition the fibres in question are not capable of communicating impressions to the sensorium, they may, however, according to Volkmann, do so in diseased states. In this way the severe pain which is sometimes felt in organs supplied by the sympathetic, does not depend so much on cerebro-spinal nerve-fibres as on an altered condition of the ganglionic fibres themselves. The number of cerebro-spinal fibres distributed to such parts is too small to explain it. Severe pain is frequently felt in bones when diseased, although, according to Volkmann, these probably receive none but sympathetic filaments. The circumstance already mentioned, that in experimenting on the sensibility of the ganglia, it has been found that these are frequently incapable of transmitting impressions until by frequent irritation they have been brought into a kind of inflammatory condition, also indicates the same thing.

All the fibres which are sent from the cerebro-spinal system to the sympathetic, through the medium of the communicating branches, are probably derived, according to Volkmann, from the posterior roots of the spinal nerves alone, and are not therefore possessed of motor properties. They hold the relation of centripetal or afferent fibres to the ganglia of the sympathetic. The motor properties of the sympathetic are therefore considered by him to be due entirely to the fibres which arise in the different ganglia. In regard to those movements which, as already stated, are excited in organs supplied with sympathetic nerves, by irritation of the central masses of the nervous system, Volkmann holds that the stimuli to contraction in these cases are not transmitted directly to the organs in which the contractions are manifested, but are first conveyed by the fibres in the rami communicantes to the ganglia of the sympathetic, where transference to the proper sympathetic fibres takes place.

Thus, then, according to Volkmann, the motor properties of the sympathetic are entirely due to the proper ganglionic fibres. The painful sensations which are sometimes felt in parts supplied by the sympathetic are due, not so much to fibres of cerebro-spinal origin as to an altered condition of the ganglionic fibres, while the fibres which are sent to the sympathetic by the cerebro-spinal system act as afferent or centripetal fibres to the different ganglionic centres, and by means of which a connection is established between the sympathetic and cerebro-spinal systems.

According to Valentin, again, both the motor and sensory properties of the sympathetic are due entirely to cerebro-spinal fibres.

It is generally admitted that the sympathetic receives fibres from the anterior as well as from the posterior roots of the cerebro-spinal nerves. The number of these fibres must, moreover, be very considerable, especially in the higher animals; it would seem probable, therefore, that the motor, and especially the sensory properties of the sympathetic are in part due to these fibres. The experiments of Budge and Waller show, almost beyond a doubt, that, in the case of the iris at least, the motor fibres which pass to it through the medium of the sympathetic are derived from the spinal cord. The circumstance, however, that the organs supplied by the sympathetic cannot be influenced by the will, and in the normal condition are removed beyond the sphere of sensation, would seem to indicate that the conducting power of these fibres must be modified by the different ganglia through which they pass in some such way as Volkmann supposes.

Are the ganglia to be regarded as centres of reflex action? By Valentin*, Longet†, and others, they are denied this property.

* Op. cit. p. 697., as quoted by Longet.
† Op. cit. p. 578.

Prochaska* seems to have attributed such properties to the ganglia, inasmuch as he explains the contraction of the heart by supposing that the impressions which are made upon the inner surface of the organ are transmitted to the ganglia by means of sensory nerves, and are there transferred to motor nerve-fibres. Grainger †, in like manner, holds that the ganglia are centres of reflex action, and moreover that each ganglion possesses a distinct so-called excito-motory system of nerves. From what has been already stated, it will be observed that Volkmann also holds the view that, in the ganglia, transference of impression from one fibre to another takes place. From his earlier experiments ‡, however, he was led to conclude that such was not the case. He found, on applying a stimulus to the surface of the intestines in a newly-killed frog, that a contraction ensued which was not confined to the part which had been stimulated, but extended for a considerable distance on either side. After destroying the spinal cord, and again applying the stimulus, he now found that the contraction produced was merely local, confining itself to the part irritated. The extended contraction first produced he believed to be due to reflex action, while the limited contraction in the second experiment he regarded as a mere stimulus movement. From the circumstance, moreover, that the former took place while the spinal cord yet remained, and the latter after it was destroyed, he concluded that it was thereby proved,—1st, that the spinal cord is the centre in which the act of reflexion takes place in the movements of the intestine; and, 2nd, that the ganglia are destitute of such power. Longet § also states that it is only while the spinal cord remains that contractions extending over large portions of the intestine can be excited by local application of stimuli, the contraction so produced limiting itself, after the spinal cord is destroyed, to the point irritated. As was shown by Henle, however, there can be no doubt that movements may be excited by application of stimulus to the surface of the intestine after the spinal cord is destroyed, which are as extended as those excited in the same way while it remains. The contractions produced by local stimuli are so similar both before and after the removal of the spinal cord as to leave no doubt that it can have no share therein. The only question is, whether the difference in character between the extended contractions and those which are limited to the point irritated are due to reflex action, or not. By Valentin and others, the extended contraction is explained in the same way as they endeavour to explain that of the heart, by supposing a particular arrangement of the muscular fibres, by means of which the contraction of one bundle acts as a stimulus to the neighbouring bundles, exciting them successively to contraction. How far this is the case it is difficult to determine; it seems, however, that the relation of the one bundle of muscular fibres to the neighbouring bundles in the intestine is not so different from what it is in the ordinary muscles as to explain the limited contractions which take place in the latter, and the extended contraction of the former, upon the application of local stimuli. The opinion of Henle*, that they are of a reflex nature, the centres of reflexion being the grey matter of the sympathetic ganglia, seems, therefore, to be the more probable. Kürschner also adopts the view that the ganglia are to be regarded as centres of reflex action. On repeating Müller's experiment of irritating the solar ganglion with potash, he observed that the movements thereby produced in the intestines did not commence at a single point, but in several different coils of the intestine at one and the same time. This may, he says, be explained in either of two ways: the stimulus had either affected directly all the motor filaments, by which these different parts of the intestine are supplied, or only a few of them; and from these few a transference took place, in the ganglion, to the others. The latter he believes to be the true explanation; for he found it is quite the same, as regards the extent of the movements, whether the irritant is strongly or slightly applied, and whether a finely-pointed rod of potash or a broad surface of the same is employed.

The contractions which are excited in the heart by application of local stimuli would seem to indicate more clearly that the ganglia are reflex centres. When a heart has just ceased pulsating application of a stimulus gives rise to a contraction affecting the entire organ, the contraction, too, taking place in the same rhythmical manner in which it takes place during life. After some time, the stimulus, when again applied, gives rise to a contraction which does not affect the entire organ, but only the particular auricle or ventricle to which it is applied, and after some time farther the same stimulus gives rise merely to local contractions. The former two seem to be, as Volkmann regards them, movements of reflex action, while the last is a mere stimulus movement. The circumstance that stimulus applied to the ventricles in such a heart gives rise to contractions which commence in the auricles, and therefore at a point distant from that to which the irritation has been applied, seems explicable only on the supposition that the impression thereby produced is conveyed to a nervous centre, and here transferred to fibres proceeding to the part in which the contraction commences.

The following experiment of Volkmann would also appear to favour the view in question. He destroyed the spinal cord in a newly beheaded frog, and satisfied himself

* Opera Minora, t. ii. p. 169., as quoted by Longet.

† Observations on the Structure and Functions of the Spinal Cord.

‡ Müller's Archiv. 1838, Einl. Theil. p. 15., &c.

§ Op. cit. p. 577.

* Froriep's Neue Notizen, band xii. p. 247., as quoted by Kürschner.

that no reflex action could be produced in the voluntary muscles. The heart was then laid bare, and during an interval of 101 minutes its pulsations were counted at fourteen different times. Five minutes after destruction of the central organs they numbered 72 per minute; thirty minutes afterwards they were 48 per minute. After this they were found to average between 45 and 51 per minute. He then crushed with the blow of a hammer one of the hind feet; and now, during the 104th minute after the spinal cord had been destroyed, counted 70 pulsations. Thus, then, two hours after the operation of destroying the spinal cord, we have a sudden increase of 20 beats in the minute, which admits of hardly any other explanation than that given by Volkmann, that it was due to the stimulus applied to the foot being reflected to the nerves of the heart through the ganglia of the sympathetic.

Influence of the sympathetic on the vegetative processes. — According to some, these processes go on independently of any influence exercised by the nervous system, while others maintain that the two are more or less intimately connected. Of the latter some believe that the sympathetic is the only part of the nervous system by which such influence is exercised, while others hold that it exercises no influence in this respect which is not also exercised by the cerebro-spinal system.

There can be no doubt that in the plant the processes of nutrition take place without the co-operation of any nervous influence; and in the same way in the embryo of all animals they go on for some time before any trace of nervous tissue has appeared. In the animal after birth, however, they appear to be more or less influenced by the nervous system. This is rendered probable by several circumstances, such as the effects of various powerful mental emotions and of morbid states of the nervous system upon digestion, on the secretion of the saliva, tears, &c.; the effects of the same upon the heart and capillary vessels. This is also shown by the changes which take place in the nutrition of parts, when the nerves by which they are supplied have been divided, or after lesions of the brain or spinal cord. Thus, as shown by Magendie, section of the fifth nerve is very quickly followed by distension of the blood-vessels and inflammation of the conjunctiva, sclerotic, and other parts of the eye, which may terminate, in the course of two or three weeks, in complete disorganisation of the eyeball. It has also been found that section of the nerves of a broken limb prevents the due formation of callus. The experiments of Drs. Sharpey and Baly on the salamander also prove that parts are reproduced much more slowly and less perfectly when the spinal cord has been destroyed to a certain extent than under opposite circumstances. When wounds are inflicted upon both limbs of an animal, and the nerves of the one limb are divided while those of the other limb are left entire, it has been found that while a lively inflammation and normal suppuration take place in the wound of the limb the nerves of which have been left entire, the wound in the limb whose nerves have been cut scarcely inflames at all, and only a thin unhealthy discharge is formed. Lesions of the spinal cord have also been observed to be followed sometimes by mortifications of the paralysed limbs, and this with such rapidity as would seem to indicate that they stand to one another in the relation of cause and effect. The tendency to sloughing observed in typhus and other diseases attended with great depression of the functions of the nervous system would also seem to indicate connection between the nutritive processes and the nervous system.

It has been already noticed that branches of the sympathetic pass along with the arteries in considerable numbers; some of them being apparently distributed to their coats, while others accompany them into the substance of the different glandular organs. It has also been stated that sympathetic fibres have been observed to join the cerebro-spinal nerves, and to run pherically with them to the different organs of animal life. From this distribution of the sympathetic, it has been held that it is in a peculiar manner connected with the nutritive processes. That it does exert an influence over the nutritive processes is seen from the effects which follow division of its branches. In addition to contraction of the pupil section of the sympathetic in the neck has also been observed to be followed by a disturbed state of the circulation in the eyeball, giving rise to swelling and inflammation of the cornea, a shrinking of the eyeball, and at the same time to an increase in the lachrymal secretion. In some of the experiments of Dr. John Reid, the injected state of the conjunctiva took place in the course of a few minutes after the operation. In a dog, in which he had divided the common trunk of the vagus and sympathetic as high up as possible, Valentin * observed that the secretions of the eye were very much increased, remaining so even after the lapse of several months. The same effects were also observed by him after extirpation of the superior cervical ganglion in the same animal. Dupuy found, on removing the superior cervical ganglion of both sides in the horse, that besides the effects above described the operation was followed by an anasarcous condition of the limbs and an eruption on the whole cutaneous surface.

Schiff† found, when the two upper thoracic ganglia in the dog or rabbit were removed, that the animal did not survive the operation for more than thirty-four hours; the heart, in the meantime, pulsated very quickly and forcibly. On examination after death, the blood-vessels of the pericardium were observed to be distended with blood,

* Op. cit. p. 423., as quoted by Longet.

† De vi motoriâ basios encephali, p. 37., as quoted by Valentin.

while a partly fluid, partly solid exudation surrounded the heart, forming in some parts adhesions between it and the pericardium.

From the experiments of Krimer it appears that division of the renal nerves gives rise to changes in the constitution of the urine. According to his observations this fluid, after the nerves have been divided, contains albumen as well as the red colouring matter of the blood, these increasing in the same proportion as the normal ingredients diminish in quantity. Similar results were also obtained by Brachet* in dividing these nerves. He cut the renal artery and with it the nerves leading to the kidney, and then connected the two extremities of the cut vessel by means of a canula so as to keep up the flow of blood. The fluid which passed off by the urethra contained fibrin and albumen as well as the red colouring matter or hæmatine. Analogous experiments were also performed by Müller and Peipers.† A ligature was applied around the renal vessels of the dog and sheep so tightly as to destroy the nerves, and again relaxed in order to allow the circulation to be re-established. Only in one case did they observe the secretion of urine continue in the kidney, the nerves of which had been destroyed, and in this case it contained blood as also hippuric acid. The kidney itself was more or less injected, and rapidly became disorganised.

As regards the influence of the sympathetic on the circulation, it has been already stated, that division of the sympathetic in the neck is followed very rapidly by distension of the vessels of the conjunctiva. From experiments lately made by Bernard, it also appears that in the rabbit the vessels of the ear on the same side in like manner become immediately distended with blood, so that the ear appears quite red, while at the same time its temperature, as well as that of the whole side of the face, rises so considerably, that the difference between it and that of the opposite side is distinctly appreciable to the touch. This experiment I have repeated several times. In a rabbit to which ether had been given, the temperature of the two ears rose to about 95° F., the vessels at the same time being much distended. The sympathetic was then divided about the middle of the neck: shortly thereafter the temperature of the ear on the side on which the nerve was not divided, sunk to 85°, and its vessels became much less distended. The temperature of the ear on the side on which the nerve had been divided, still continued as high as 95°, its vessels also remained distended, and were felt pulsating forcibly. On examining the two ears an hour or so afterwards the temperature of that upon the side on which the nerve had been divided, was still felt to be distinctly warmer than the other: its vessels were also still distended, and pulsating forcibly. How long the effects produced upon the temperature and blood-vessels continue I have not been able to ascertain: they are certainly not so permanent as the contraction of the pupil. While this remains contracted for weeks, or even months, no difference in the condition of the two ears can be distinguished a week or so after the nerve has been divided.*

* Op. cit. p. 326.

† De Nervorum in Secretiones Actione, p. 26.

* The elevation of temperature, according to Bernard, begins immediately after the nerve is divided, and is so quickly developed that in a few minutes, in certain circumstances, the difference in temperature of the two sides of the head may rise to 4° or 5° centigrade. This difference of temperature is perfectly appreciable to the hand, but is better determined by introducing a small thermometer into the nostril or ear of the animal. Removal of the superior cervical ganglion is followed by the same effects as section of the sympathetic cord, only these effects are always more rapid, more intense, and more durable. After section of the sympathetic cord in rabbits the phenomena of excess of sensibility and calorification are scarcely observable beyond five to eighteen days, while in dogs they may continue for six weeks or two months. After ablation of the ganglia in these animals the persistance of the phenomena may be regarded as indefinite: in a dog in which the superior cervical ganglion of the left side had been removed all the phenomena of excess of sensibility and calorification due to that operation were very intense a year and a half after the extirpation of the ganglion, when the animal was sacrificed for other purposes. The temperature of the side of the head on which the operation has been performed is nearly the same as that of the central parts of the body, such as the abdomen, thorax, or rectum; sometimes, however, it is higher, being 40°, while the temperature of the internal parts is 38° to 39°.

The increase of temperature is also attended by an increase in the activity of the circulation, as is very distinctly seen in the ear of the rabbit. But in the following days, or even on the day after the operation, the vascular turgescence diminishes considerably, or disappears, while the heat of the face continues to be very well developed. It is found, by passing the bulb of a small thermometer into incisions properly made, that the elevation of temperature observed on the superficial parts of the head extends to the deeper parts as well, and even into the cavity of the cranium and substance of the brain. This is better observed after extirpation of the superior cervical ganglion. The blood itself, which returns from parts so heated, also possesses a higher temperature. The side of the head on which the temperature has been so raised, presents also a greater resistance to the effects of heat and cold, when the animal is placed in a stove where the ambient heat is greater than that of the body; while the sound side becomes warmer, the other does not. When placed in a colder medium than its own body, the whole side loses temperature more rapidly than the other. There is also a sort of exaltation of vitality on the side on which the operation has been performed, the involuntary movements continuing longer on this side than in other parts of the body.

When the cephalic extremity of the cut sympathetic nerve in a dog is galvanised, not only does the pupil become larger, but all the other phenomena which followed division of the nerve disappear, and the opposite take place; the pupil becomes larger than that of the opposite side; the eyeball projects; the vascularisation disappears; and the temperature sinks below normal. When the galvanisation is stopped, then the phenomena caused by section of the nerve reappear.

By Walter and Brown Sequard the elevation of temperature is attributed to an increased afflux of

The experiments of Walther on the frog would also indicate that the circulation is more or less influenced by the sympathetic.* When the fibres which are sent by the sympathetic to the nerves of the lumbar plexus were divided, he found, on examining the circulation in the web of the foot, that, although at first undisturbed, it very soon afterwards increased in rapidity. The capillaries appeared to be dilated, and contained fewer blood corpuscles than corresponded to their calibre; the increase in their diameter equalled from one sixth to one eighth of the calibre of the vessel. After a time the rapidity of the circulation again diminished, and in some parts it became stagnant. Bidder †, on the other hand, could not in his experiments satisfy himself that any dilatation of the capillary vessels took place. Walther, however, has performed the experiment so frequently, and so uniformly with the same result, that he regards the dilatation of the capillary vessels as constant.

There are, moreover, certain experiments made by Valentin which show that the branches of the sympathetic which are distributed to the walls of the blood-vessels, exercise an influence over their contractions. Thus, when stimulus was applied to the thoracic portion of the sympathetic in the horse, he observed that the thoracic aorta and thoracic duct diminished in calibre to a much greater extent than could be attributed to the mere action of the atmospheric air. In a newly killed young rabbit, in which the part of the vena cava next the heart, as well as the right auricle were pulsating, he found on applying the wires of the magneto-electric apparatus to the right ventricles, that all contraction in the vessel immediately ceased.

Whatever influence the nervous system exercises over the processes of nutrition, it would seem that the sympathetic cannot be regarded as the only nerve concerned : the cerebro-spinal system also appears to share therein. In addition to what has been already stated, p. 470., there are also other facts which favour such a view. Thus Magendie found that, where the spinal cord was divided in the region of the neck, a disorganisation of the eyeball followed, similar to that which ensues upon division of the fifth nerve. Schiff* has observed that when the crus cerebri or optic thalamus in the rabbit was cut across, the secretions of the intestinal canal become altered; the excrements are slimy and mingled with blood ; the digestion is interfered with, the animal, towards the end of the first week, losing all appetite for food. After death the mucous membrane of the stomach and bronchi was found to be more or less injected with blood, the former also being softened. Similar appearances were also observed in the upper half of the small intestine. That, moreover, the influence exercised by the sympathetic over these processes does not differ from that exercised by the cerebro-spinal system, is indicated by the circumstance that several glandular organs, such as the mammary and salivary glands, derive their nerves chiefly from cerebro-spinal nerves.

From the experiments of Schiff and others it would appear, however, that the ganglionic system of nerves is more intimately connected with these processes than the strictly cerebro-spinal nerves are. Thus, Schiff found, in regard to the fifth nerve, that when it was divided between the brain and Gasserian ganglion, the destruction of the textures of the eyeball follow more slowly then when it is divided between the ganglion and the eye. In the frog, also, when the lumbar plexus was divided, the animal continued for two or three months without any disturbance being observed in the nutrition of the limb ; but when several of the lumbar ganglia were removed, dropsical effusion into the abdominal cavity, and inflammation of the peritoneum, ending in the death of the animal, ensued in the course of two weeks.† Axmann ‡, as quoted by Valentin, divided at their roots the nerves which supply the posterior extremity in the frog, but in no instance observed that the operation was followed by any disturbance in the nutritive processes: wounds of the soft textures as well as of the bones healed as rapidly

blood due to paralysis of the blood vessels. Bernard, on the other hand, believes that the phenomena are not due to the effects of paralysis of the blood vessels, but are active; they are of the same nature as the vascular turgescence which arises in a secreting organ when it passes from a state of repose to an active discharge of function, and resemble the afflux of blood, and increased sensibility around a recent wound or foreign body in the living textures; phenomena which are not due to mere paralysis of the arteries.

The sympathetic is the only nerve section of which is followed by an exaltation of temperature. Section of the fifth nerve Bernard found to be followed by diminution of temperature on the corresponding side of the head. When the facial nerve was divided at its exit from the cranium, an elevation of temperature took place on the paralysed side; this was increased when the sympathetics on the same side were also divided. If the facial was alone divided then, after a few days, the temperature returned to an equality on both sides of the face. The calorification produced by section of the facial nerve Bernard attributes to the division of sympathetic fibres which join the nerve during its course through the temporal bone. He also found that when the anterior or posterior roots of the spinal nerves going to form the sacral plexus were divided, the temperature was not increased but diminished. See Monthly Journal of Med. Science, March, 1854. Original paper in Gazette Médicale, Janvier, 1854.

Budge finds that removal of the portion of the spinal cord termed by him the ciliospinal region, is attended by an increase of temperature on the corresponding side of the head in the same manner as when the sympathetic is divided in the neck.

* Müller's Archiv. 1844, p. 448.

† Henle and Pfeuffer's Zeitschrift, band iv. p. 353.

* De vi motoriâ basios encephali, p. 37., as quoted by Valentin.

† Op. cit. p. 37.

‡ De Gangliorum Systematis Structurâ penitiori ejusque Functionibus. Berlin. 1847. p. 248.

as in the sound leg. When he divided the trunk of the lumbar nerves below the spinal ganglia the skin became gradually pale, its pigment cells diminishing to mere points; the structures softened; the liver and kidney no longer secreted; while dropsical effusions, containing the elements of the bile and uric acid, at the same time took place. The blood corpuscles also gradually disappeared. The vessels of the spinal cord and of its membranes became very much distended with blood. When the lower portion of the sympathetic cord on either side was removed, the blood-vessels of the hind leg and pelvic organs became highly congested; the contractility of the muscular tissue in the legs and in the pelvic organs disappeared. Blood was extravasated into the bladder and rectum, secretion of urine ceased, and dropsical effusions took place. The circumstance that section of sensory nerves is followed by derangement in the nutritive processes much more quickly than similar lesions of motor nerves is also explained by Volkmann as due to the fact of the former containing a comparatively larger number of fine or sympathetic fibres.

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(*J. Drummond.*)

TEGUMENTARY ORGANS. In endeavouring to deal with so large a subject as the tegumentary organs of animals, within the limits of an article like the present, it appeared advisable not to attempt to enter into minutiæ of detail (which indeed fall more properly within the province of those who treat of the special classes), but so far as possible to regard these organs as a system in the sense of Bichât — as a sort of zoological class — whose members, the tegumentary organs of particular animals, are but special modifications of one general plan. In reflecting how this might best be done, however, I was met at the outset by certain difficulties and perplexities whose solution appears to me to be essential to any philosophical treatment of the subject, and to the consideration of which I, therefore, propose to devote the following *Preliminary Section.*

§ 1. My first difficulty was to find an answer to the question,—What constitutes a tegumentary organ as distinguished from any other?

The most obvious definition of an *integument* or *tegumentary organ* is, of course, — that which forms the external covering of any animal — *viscus*, on the other hand, being that which is contained. More strictly, it may be said that the integument constitutes that free surface of an animal which is external to the edges of the oral and anal apertures, or where the former alone exists, to *its* edge. Now these definitions are perfectly sufficient so far as surface is concerned; but suppose we make a section perpendicular to the surface, where does integument cease, and where does viscus begin? So far as I am aware, no elucidation of this point has hitherto been undertaken, and yet, for want of it, the greatest confusion prevails in the nomenclature of those organs which constitute the outer wall of the animal frame.

Intimately connected with this question, and indeed forming a part of it, is a second. In man and the higher animals, there is an universally recognised distinction of the integument into two portions,—the *epidermis* and the *derma;* and these terms have been extended to all animals. But, if we inquire what constitutes an epidermis, and what a derma, no definite answer is to be met with. It may be said that the derma is vascular, while the epidermis is nonvascular; or that the epidermis is a simple cellular horny structure, while the derma is complex and fibrous; but these characters, applicable enough among the higher animals, fail completely with the lower.

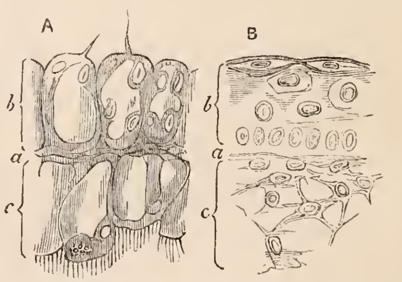
Thus, in the majority of the Invertebrata, the derma cannot be said to be vascular, while, on the other hand, the epidermis, or its representative, assumes the structure of fibrous tissue, bone, cartilage, dentine, and enamel, — acquires, in fact, the utmost complexity, and, instead of possessing a horny nature, contains chitin, cellulose or calcareous salts.

Following Mr. Bowman, — who, of course, when he wrote his well-known article on "Mucous Membrane," in this Cyclopædia, could not contemplate the new questions to which the progress of ten years would give rise,—many regard that which is external to a "basement membrane" as epidermic, that which is internal to it, as dermic structure. This test, however, fails us where we most want it; for among the lower animals, and in some integumentary organs among the higher, membranes identical in structure, or rather in structurelessness, with "basement" membranes, may be met with, forming the surface of what are assuredly epidermic organs.

I believe that here, as elsewhere, the only ultimate appeal lies to development, both as it occurs in the embryo and as it goes on in the adult. What, in fact, is the first process which takes place in the embryo, when the germinal disc is once formed? It is a separation into two layers, by the setting up within the outer portion of the primitive germ of a process of growth independent of that in the inner portion. Where these two areæ or planes of growth, as they might be called, meet, the germ readily separates into two portions, the outer of which is the so-called *serous layer*, the primordial tegumentary system; while the inner is the *mucous layer*, the primordial viscus. Of course each of these, while *actually* integument and intestine, represents *potentially* a great deal more,—the former, for instance, in the higher animals becoming eventually differentiated into the proper tegumentary system and a great part of the nervous, the muscular, and the vascular systems; but what I wish to direct attention to at this moment, is the fact, that this first differentiation into integument and viscus proceeds from the setting up of two independent lines, or rather planes of growth, in the germinal membranes.

In the Hydra and Hydroid Polypes generally, we have the essence of this embryonic state as a persistent condition. If, in fact, the body or almost any organ of one of these animals be examined, it will be found (*see* Memoir on the Structure of the Medusæ, Phil. Trans. 1849) to be composed of two distinct membranes, an inner and an outer (*fig.* 303. A). The junction between the two is distinctly marked by a clear line, which would elsewhere be called a basement membrane (*a*). External and internal to this, there is a layer of young tissue, consisting of a homogeneous periplast with minute imbedded endoplasts ("nuclei"). As we proceed towards the free surface, we find that a process of vacuolation and cellulation takes place in the periplast, until the coarsely cellular appearance with which every one is acquainted is produced.

Fig. 303.



A, hydra; *b*, outer membrane; *c*, inner membrane.

B, young mammal; *b*, epidermis; *c*, derma.

In the Hydra, then, we have the whole thickness of the body divided into two portions by a line, on each side of which, inwards and outwards, there is an increasing histological metamorphosis or differentiation. There is a median *plane of no differentiation*, as it might be termed, external and internal to which, is a zone of *indifferent tissue*, while, still more remote again, is a zone of *metamorphosed tissue*. The absolute structure of the two layers thus produced is very similar *, so much so, that, as is well known, either may perform for a time the function of the other. The distinction between the integument and the mucous membrane in a morphological point of view, however, is as strongly marked as in the most complex animal. The integument, in fact, grows from within outwards—it is endogenous, its youngest portions being internal: the mucous membrane, on the other hand, grows from without inwards — its youngest portion is external, and it is, therefore, exogenous.

We have here, I believe, the fundamental, and the only essential distinction, between true *integumentary* or "*epidermic*" structures and all others. *An integumentary or epidermic organ forms or has formed a part of the external surface, and grows endogenously; its youngest portion and plane of no differentiation being directed inwards.*

If, for instance, we compare the young skin of a mammal with the body of the Hydra, we shall find precisely the same planes and zones.

Fig. 303. B, represents a perpendicular section of the integuments of a fœtal lamb $3\frac{1}{4}$ inches long. (A) marks the position of the line of no differentiation separating the epidermis from the derma; on the outer side of that line lie the close-set endoplasts of the deepest layer (*rete*) of the epidermis, which are disposed somewhat perpendicularly to the surface. On the inner side are the less approximated endoplasts of the outer youngest layer of the derma, more or less parallel to the surface. From *a* to *b*, lies the epidermic area of metamorphosis, the indifferent tissue becoming gradually converted into flattened horny cells. From *a* to *c*, on the other hand, is the dermic area of metamorphosis, the indifferent tissue gradually changing into connective tissue.

It will be observed here, that as the whole serous layer of the germ corresponds in structure with the epidermis only, of the fully formed animal, so the whole integument of the Hydra corresponds with what is usually considered as only a portion of the integument—the *epidermis*—of the mammal. The derma, or true skin of the latter, would not come at all under our present definition of integument, since it has all the morphological characters of the mucous layer of the Hydra, or of the germ; *i. e.* its youngest layer is external, its growth is exogenous, and the metamorphosis of its tissue takes place from within outwards.

In fact, in all animals higher than the Hydroid Polypes (possessing therefore a visceral cavity) we find a complication of structure, corresponding with that which is produced in the germ, when the "*membrana intermedia*" divides into its parietal and intestinal laminæ. Compared with the Hydroid Polypes, the higher forms are double animals, and a section of their bodies is, morphologically speaking, like a section of two Hydræ, one contained within the other. Both the intestinal parietes, and those of the body, present the same distinction into a central *plane of no differentiation*, from which growth and metamorphosis proceed inward and outward on the two respective surfaces, as that observed in the parietes of the Hydra.

The formation of this so-called membrana intermedia, in fact, appears to result from a repetition of the process which gave rise to the two primary layers of the germ. The previously central *plane of no differentiation* is replaced by two others, from which growth and metamorphosis proceed in the same way. The result is, of course, the division of the germ into three layers — a central and two superficial (inner and outer) planes of metamorphosed tissue — and two planes, whence growth and metamorphosis proceed.

It results from all this, that, among the higher animals, the true homologue of the integument of the Hydra is the epidermic layer alone. But it would be exceedingly inconvenient to change the accepted meaning of "Integument" on this ground; and, therefore, I shall, throughout the present article, consider as integument — *the outermost plane of indifferent tissue in the animal body, with its external and internal areæ of metamorphosis collectively; these being simply the expressions of two processes of growth in opposite directions, and their line of contact.*

It must not be supposed that this phraseology involves any hypothetical views: the fact that any integumentary organ consists of these three portions will be found to be either distinctly stated or implied by all writers, and is indeed obvious enough on inspection. But though the facts be old enough, this expression of them is unfortunately so new, that I know of no existing terminology by which it can be properly enunciated. The term "Epidermis," for instance, at present, though it denotes the important character of the direction of growth to which I refer, implies even more strongly the simple cellular structure of an organ; so that to speak of "Epidermic" bony or fibrous tissue would sound almost contradictory. Again, all these distinctions, which have been shown to exist between the two elements of the integument, equally hold good with regard to the mucous membranes. Now we have a term "Epithelium" for the epidermic element of the latter; but there is, as far as I know, none for the element which corresponds with the derma. Nor have we any word for the boundary line between the endogenous and exogenous areæ of growth — the term "basement membrane" expressing only an accidental character of the tissue immediately on one or the other sides of that line.

Although with great reluctance, then, I feel compelled to propose two or three new terms, which may have general application, not only to the integumentary organs, but to all other

* Though not, as it is commonly said, identical.

membranes which possess free surfaces and definite directions of growth and metamorphosis.

The boundary line — passing through indifferent tissue — between any two such opposite areæ of growth and metamorphosis, I term the *Protomorphic line*. The whole external (free) area of metamorphosis I call the *Ecderon;* the entire internal (deep) area of metamorphosis, the *Enderon.*

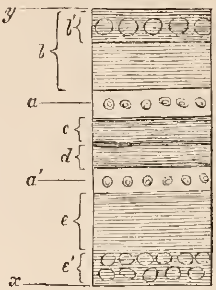
It will be observed that these definitions rest wholly upon the *mode of growth*, and leave altogether out of consideration the *structure* of the resulting tissue. In fact, as I have already said, an extensive study of the integumentary organs convinces one at once that mere structure affords no base for homology; the ecderon, for instance, presenting every variety from the structurelessness of a homogeneous membrane, as in the Tæniadæ, to the complex combination of the so-called enamel, dentine and bone, in the scales of Placoid Fishes.

It is, I venture to think, no small evidence in favour of the importance of these considerations that they enable us to carry still further the doctrine of the identity of structure of plants and animals sketched by Caspar Wolff, and developed in our own times by Schwann. If we make a transverse section of the growing limb of a vertebrate animal, leaving out of consideration, for the moment, the vessels, nerves, and muscles, we observe from the surface inwards, 1st, the ecderonic area of metamorphosis; 2nd, the integumentary protomorphic line; 3rd, the enderonic area of metamorphosis; 4th, the periosteal area of metamorphosis; 5th, the protomorphic line, formed by the indifferent tissue between periosteum and bone; 6th, the osteal area of metamorphosis, within which lies, 7th, the cartilage resulting from the metamorphosis of the tissue of the primitive axis of the limb.

Now, if we compare this with the growing shoot of a young exogenous plant, we meet with exactly the same series from without inwards. There is, 1st, the epidermis, which commonly becomes replaced by a cork or peridermal layer, just as the primary epidermis over a nail is thrust aside by the subjacent and subsequently-formed horny matter; or, as the horny "epidermis" of a Skate is pushed aside and replaced by the calcareous placoid spine. Beneath this lies, 2nd, a protomorphic (or *cambial*) line, from which metamorphosis into periderma goes on outwards, while inwards it passes into, 3rd, the metamorphosed tissue of the mesophlœum. Next to this comes, 4th, the metamorphic area of the endophlœum or liber; within which is, 5th, the protomorphic line of the cambium, which becomes metamorphosed on its inner surface into, 6th, the wood; within which lies, 7th, the pith, the result of the metamorphosis of the primitive axis of the shoot.

I have endeavoured to render these relations obvious by the diagram (*fig.* 304.), which may be taken for a section from centre to surface of a fœtal limb, or of an exogenous branch. *a*, outer protomorphic line between epidermis or periderma and mesophlœnm in the plant;

Fig. 304.



between ecderon and enderon in the animal; *a'*, inner protomorphic line between liber and wood of plant, between bone and periosteum of animal; *b*, *b'*, cork and epidermic layers of plant; cellular epidermis and scale of animal, fish, *e.g.*; *c*, mesophlœum, enderon (derma); *d*, liber, periosteum; *e*, *e'*, wood and pith, bone and cartilage; *x*, axis; *y*, surface.

The consideration of vegetable structures will aid us even further in understanding the manner in which the different varieties of integumentary organs, with which we shall meet, are formed. For it is well known that the outer covering of a plant may ultimately be constituted in one of three ways. 1. The original cellular ecderon may persist unchanged. 2. The "epiderm" persisting, a laminated, but otherwise structureless "*cuticula*," may be developed upon its outer surface, attaining sometimes a very considerable thickness. 3. The original epidermis is cast off, its place being taken by the development of a new layer of different, usually suberous constitution, beneath it, which then goes on growing endogenously, and constitutes the permanent integumentary surface. Now, we find a precise parallel for all these conditions in animals. In the soft integument of most Mollusca and Vertebrata the first condition obtains, the general surface of the integument being constituted by the cellular "epidermis."

In the Annulosa, on the other hand, the integument has certainly, in many cases, and I think probably in the great majority, the character of a vegetable cuticle, consisting as it does of layers developed from the outer surface of the cellular ecderon. In this way also I believe that all molluscan shells are formed.

Lastly, the fish-scale produced altogether beneath the cellular ecderon or epidermis, but growing endogenously after the manner of a true ecderonic structure, appears to be precisely analogous to the corky periderma of the plant; and as the latter, though it is not the original epidermis, takes its place and grows in the same way, so in the fish the scale, which is assuredly not a calcification of the cellular ecderon, yet represents it both in position and in mode of growth.

§ 2. *Morphology of the integuments.*— In the embryonic state of all animals, and in the adult condition of many of the lower forms, the integument, constituted as above defined, forms a continuous investment over the surface of the body without any important processes or irregularities. Such is the case in many of the Worms, Polypes, and lower Mollusca. From such simple forms of integument as these the most rudimentary kinds of appendages or tegumentary organs are produced in one of two ways,—either the outer portion of the ecderon is thickened, and as a spine or as a plate projects beyond the common surface—*e. g.* cells of Hydroid and Polyzoic Polypes ; or the whole integument is developed into a spine-like or plate-shaped process, as in the so-called "bracts" of the Diphydæ, and in all the spines, hairs, and scales of the Insecta, Crustacea, and Arachnida.

The shells and plates of Mollusca and Articulata belong principally to the former division, being simple laminated thickenings of the outer portion of the ecderon. In the Vertebrata the integument but rarely possesses appendages of so simple a nature. Simple plates of this kind, however, coat the surface of the beaver's tail, in which animal, according to Heusinger, "the epidermis is divided by a great number of clefts into hexagonal portions 4 lines long, whose whole edges adhere to the cutis. They usually consist of a couple of superimposed laminæ identical in structure with the rest of the epidermis" (*l. c.* p. 168.). The polygonal horny plates of the Chelonia are of the same nature. The scales on the under surface of the tail of the rat and other rodents, and on the tarsi of birds, are similarly constituted; but here one edge is thrown up, and we have a transition to the scales of the Pangolin,—to those of Ophidia and Sauria,—and to the nails, claws, hoofs, and hollow horns of Mammals, and the horny sheaths of the beak of Birds, all of which are constructed on essentially the same plan, being diverticula of the whole integument, the outer layer of whose ecderon has undergone horny metamorphosis.

Among these the nails, horns, and hoofs of mammalia present certain complexities of arrangement which entitle them to particular notice.

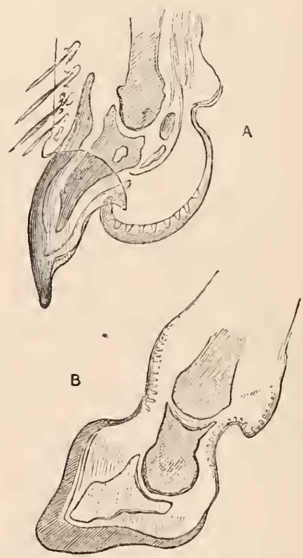
Nails are flattened horny plates developed from the upper surface of the phalangeal integument only; they are free at their distal extremities, but laterally and at their proximal ends they are enclosed within raised ridges of the whole integuments, the *nail walls.* The enderon beneath them in the space which is called the "bed of the nail" is raised into parallel longitudinal ridges or laminæ, which fit into corresponding depressions of the under surface of the ecderon.

Claws are nails which embrace a larger portion of the phalanx, being developed, not merely from its upper surface, but also from its extremity, and extending far round on its sides. In the dog and cat (*fig.* 305. A) the bed of the claw is laminated as in man, but presents no papillæ (Gurlt), and a bony plate extends from the last phalanx into the posterior fold of the nail.

The transition from the claw to the *hoof* is readily understood if we suppose the terminal portion of the former to be blunt and cylindrical, instead of pointed and conical (*fig.* 305.). The elephant and rhinoceros do in fact afford an actual passage from the nail to the hoof, inasmuch as their very flat nails are continuous at their edges with the solid horny covering of the sole (Heusinger).

The solipede hoof has been described in the article SOLIPEDIA; we need therefore only remark here that the *wall* corresponds with the nail in man, and may, by maceration, be separated from the sole and frog, which are developed from the termination and posterior surface of the phalanx. The ridge or "bourrelet" at the upper margin of the wall answers to the posterior nail-wall, and, as in the nail, the horny upper layer of the "epidermis" is continued on to the hoof from it. The structure of the bed of the hoof differs in its different parts. That portion which corresponds with the sole and frog merely presents papillæ, which fit into depressions of the horny ecderon; that which corresponds with the wall is produced into lamellæ like those of the bed of the nail, so that the deep surface of the wall is laminated. In addition, however, long papillæ extend from the "bourrelet" through the superficial portion of the wall, so that, on section, it presents a superficial series of canals, around which the horny matter is disposed in concentric layers.

Fig. 305.



A. Section of the foot in a kitten. B. In a fœtal lamb.

Each half of the hoof of a ruminant (*fig.* 305. B), or of the pig, corresponds in general structure with the entire hoof of a solipede, except that the frog is rudimentary. The horny ecderon presents both tubuli and laminæ.

The excrescences on the inner surface of the leg of the horse are identical with the sole of the foot in structure — consisting of a horny mass penetrated by long papillæ.

The hollow *horns* of the Ruminantia are, to all intents and purposes, *Claws*. The superficial cellular ecderon (epidermis) is continued upon them, and, when this is removed, we come to a laminated fibrous horny mass, which is formed and increased by apposition from the subjacent process of the enderon, supported by its bony axis — a process of the frontal bone. The enderon has neither villi nor lamellæ, presenting only small irregular ridges (Gurlt).

The *horn* of the rhinoceros is commonly said to be constituted by a mass of hairs which have coalesced. However, it consists of an aggregation of tubes, round which the horny matter is arranged in concentric laminæ, as in the horny excrescence of the horse's leg; and as there is no evidence of its having ever been enclosed within a sac, it is more probable that it belongs to the series of the claws and nails.

Glands, hairs, and feathers. — The *Hairs* and *Spines* of mammals, the *Feathers* of birds, and the *Integumentary Glands* agree in one essential point, that their development is preceded by that of an involution of the ecderon, within which they are formed, and by which the former are, at first, entirely enclosed.

At an early period, the rudiments of the hairs, and those of the cutaneous glands of a fœtal mammal, are indistinguishable. They alike consist of solid processes of the ecderon, consisting of a homogeneous matrix, in which lie closely-set endoplasts, bounded internally by a clear, narrow, transparent "basement membrane," which at once separates them from, and connects them with, the enderon.* Externally these processes are continuous with the rete mucosum of the ecderon. In the fœtal lamb, in which I have carefully traced the development of these processes, they increase in size without change of structure, until, in the ordinary hairs, they have attained a length of $\frac{1}{150}$ inch; for the vibrissæ, that of $\frac{1}{60}$ inch. Having reached this length, it is seen that an accumulation of the indifferent tissue of the enderon has taken place around their cœcal ends, which gradually become pushed in, so that, from being rounded, they appear truncated in section, and present a bulb with a hemispherical involution, the rudiment of the papilla. In the ordinary hair no special accumulation of indifferent tissue takes place around the body of the involution; but in the vibrissæ, which are ultimately to possess a thick outer capsule, its foundation appears in this form, and a capillary loop may be seen penetrating the rudimentary papilla.

In the furthest advanced vibrissæ the tissue of the axis of the sac was converted into horny cells, the rudiment of the "fenestrated" or of the inner, horny rootsheath. Over the papilla the rudiment of the hair shaft was indicated by a conical process, horny at its apex and marked by radiating lines. Finally, on each side of the neck of the sac there was a bulging process, the centre of which was occupied by a mass of fatty-looking granules, the future sebaceous glands of the hair.

Hairs are not normally susceptible of indefinite growth, but have, like the teeth, a fixed form to attain. This form is always that of a more or less elongated spindle, inasmuch as the hairs are sharp at their points, becoming broader and thicker in the middle, and diminishing again to their proximal ends. When fully formed, and ready to fall out, in fact, this end of the hair is either pointed, or more or less ragged and brush-like.

As soon as the finishing process of any hair begins the foundation of a new one is laid by the development of a diverticulum of the outer rootsheath towards its base, in which a young hair is developed, in the manner already described, and gradually pushes out the old one.

The varieties of form and appearance presented by the hairs of animals (for which see the works of Hensinger, Eble, Busk, and Quekett, cited at the end of this article) are produced; 1st, by the relative proportions of the medullary and cortical substances, and the arrangement of the former with respect to the latter. Thus the peculiar appearance of Rodent hairs is due to the disposition of the medullary substance. 2nd, by the development of the cuticular layer, whence arise the whorled scales of bat's hair — the imbricated plates of seal's hair, &c.; 3rd, by the shape of the shaft, which may be cylindrical, as in ordinary hair of the head in man; or evenly flattened, as in the short curly hairs; or narrow and cylindrical below, and wide and flattened above, as in the hairs of the deer tribe. The spines of certain mammals, such as *Hystrix* and *Erinaceus*, present some interesting peculiarities of form; offering, as they do, a sort of transition between hairs and feathers.*

The porcupine's "quill," as it is called, is a cylindrical tube which gradually diminishes to a point above and below. At its apex the cavity of the quill is simply conical, but lower down its section becomes polygonal, and, the angles of the polygon being prolonged, resembles a four-rayed star. Still further towards the root of the quill, each ray of the star divides into two secondary rays, and then the secondary rays subdivide into two tertiary rays; so that eventually the cavity of the spine is a complicated star with four and twenty branches. Below its middle, the quill diminishes in diameter, and at the same time the complexity of its internal cavity likewise dis-

* The further development of the *glands* will be most conveniently considered, together with their histological structure, below.

* See Bröcker (Reichert's Bericht, 1849), from whom the account in the text is taken, though the main points have been independently verified.

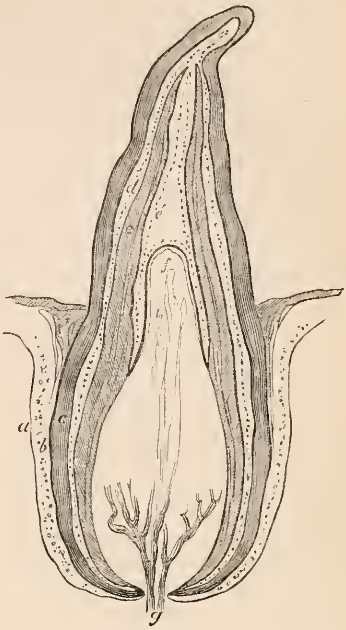
appears, the tertiary rays disappearing first, and then the secondary, &c., until at last the cavity is circular as at the apex. The boundary of the quill cavity is immediately formed by medullary substance; but the cortical substance follows to a certain extent the contour of the inner cavity, so that in a transverse section of the middle of the quill the cortical substance presents the same general outline as the medullary, though its processes and insections are less marked.

In the adult condition, the central cavity is filled by an irregular horny mass, which Reichert and Bröcker regard as the dried-up pulp, but which is probably, as in the feather (*vide infra*), simply the last horny product of the pulp, filling up the space which the latter once occupied; for it is certain that every portion of the porcupine quill has, like every portion of a feather, at one time constituted a cap over the corresponding portion of its pulp. The pulp, in fact, commences like that of a feather, as a smooth conical process upon which the apex of the quill is moulded. As it grows, however, the pulp assumes an angular form, and then, as that of a feather would do, becomes produced into lamellæ. By the constant production of new elements at the surface of these lamellæ and their cornification, the "quill" is produced, and retains internally the impression of the mould on which it was formed. Apart from the arrangement of the lamellæ, the principal difference from a feather which the "quill" presents, is simply that it does not, as it is formed, split up along the lines of the lamellæ of the pulp.

In its main features, the process of development of *feathers* is identical with that of hairs. A solid diverticulum of the ecderon is first formed, within which the primary change consists in the metamorphosis of certain median cells into a cone composed of horny plates. There is thus formed, as in the hair, an outer rootsheath, resembling and continuous with the *rete mucosum*, an inner rootsheath, and a central papilla, the so-called matrix of the feather (*fig.* 306.).

The horny rootsheath (*fig.* 306. *c*) attains a very considerable thickness, and instead of stopping short of the mouth of the sac, as in the hair, its outer end is for a considerable time pushed forwards by its basal growth *pari passu* with that of the feather; so that it eventually projects for a considerable distance beyond the surface. Finally, it opens and allows of the passage of the feather, which grows through it, the horny layer ultimately forming a true rootsheath around the quill. Like the rootsheath of the hair, this structure consists of two layers, an outer (*c*), denser and harder, and an inner (*d*), softer and more flexible. The latter from being marked by the projecting barbs of the young feather has been called the *striated* sheath. Both layers, however, have the same essential structure, being composed of rounded or polygonal horny plates, whose endoplasts are often distinctly retained even in the outer layers. The histological metamorphosis of the feather will be described below, but the manner in which it acquires its ultimate complex general figure requires particular attention. Referring for further de-

Fig. 306.



Sectional view of feather in its sac: Fowl.
e, barb; *f*, pulp; *g*, venal.

tails to the article AVES, I may state here, that every feather consists of the following parts:— *the quill* continuous with the *shaft*, or central axis of the feather, which supports the horizontally expanded *vane*, consisting of numerous long, narrow, flattened laminæ; the *barbs* or primary rays, pointed at their extremities and arranged with their edges upwards and downwards more or less perpendicularly on the shaft. Arranged in a similar manner on the barbs, are the *barbules*, which therefore are disposed more or less parallel to the shaft; from the sides of these, lastly, project short, toothed, curved, interlocking *processes*.

All parts of the feather are solid, except the quill, which is hollow and occupied only by a dry shrivelled mass, the *pith*, in its upper part, while below, during life, it receives the pulp. Superiorly, on the under side, where the quill joins the shaft, there is a small aperture, which communicates with the interior, with a short canal in the shaft, and with a groove which runs along its under surface.

It may be well to remember that the apex of a barbule resembles in structure one of its own processes; that of a barb, one of its barbules; that of the shaft, one of its barbs.

The development of this complicated organ from its *matrix* or *pulp* takes place very simply, by a sort of exaggeration of the combination of hair development with that of the nails, which has already been described as occurring in the spines of the porcupine.

On the surface of the feather-pulp a series of ridges are developed, running pretty nearly parallel with one another from an antero-posterior groove upon the upper surface, which marks the position of the future shaft, to a line parallel with that groove upon the under surface or the process, which is called the *raphe*. These ridges, therefore, bound as many grooves which branch off from the medio-dorsal groove, becoming gradually shallower, to the raphe. These secondary grooves, as they might be termed, however, are not themselves simple; their walls, the ridges, being again produced into short parallel laminæ, and therefore giving rise to tertiary grooves, branching off from the secondary ones. Now, the whole surface of the matrix being covered by an ecderonic layer in process of conversion into the cortical and medullary substances of the feather, the primary groove becomes filled by the end of the shaft; the secondary grooves by the terminal barbs, the tertiary grooves by their barbules, while the processes appear to be outgrowths from these. Were all this conical horny cap to remain entire, the result would be a very complex sort of porcupine's quill; instead of this, however, it breaks up along the line of each ridge, and so we have a feather.

The extremity of the feather being thus constituted, how is its remaining length developed? According to Reichert, the whole pulp elongates, and as fast as a portion of the feather is completed, the corresponding segment of the pulp dries up, constituting for the vane what has been called the *inner striated membrane* (*e′*). However, I believe that this is not the case, the inner striated membrane being, like the outer, a mass of cornified cells detached from the surface of the pulp, just as we shall see the pith of the shaft to be, though this has been also declared by Reichert to be dried-up pulp. I believe that the growth of the feather, on the other hand, resembles that of the hairs and nails; viz. the extremity as it is finished, is pushed up by the growth of the base, the pulp only supplying materials from its surface; and I account for the inner striated membrane by supposing that a comparatively imperfect development of horny cell membranes takes place from that surface of the pulp which would otherwise be left bare, when the terminal cone or plume of the feather is pushed away. When the development of the shaft has gone on in this manner for a longer or shorter time, according to the length of the feather, a change takes place. The primary groove, which has gradually widened with the width of the shaft (to the exclusion of the secondary grooves, which gradually shorten and ultimately disappear) becoming shallower, extends all round the pulp, and the formation of medullary feather substance ceases, that of cortical substance alone remaining. Thus is the hollow quill formed, and its edges, not quite closing above, leave the minute umbilical aperture by which the inner striated membrane is continued into the "pith" of the quill. This pith is produced by the throwing off of successive transverse horny partitions from the apex of the pulp, as the quill is pushed beyond it; thus protecting itself from the air admitted by the umbilical aperture, and which is visible, occupying the chambers thus formed (*fig.* 316. G).

A full description of the various forms of feathers is given in the article AVES in a former portion of this work, to which the reader is referred.

There can be no question as to the relations of the integumentary organs hitherto described to the primary constituents of the integuments, but it is different with regard to those calcified tegumentary appendages, the *scales* of Fishes, and the so-called "*dermal*" *calcified plates* of Reptilia and Mammalia. One point is quite certain with regard to these appendages, that they are not, like the calcified shells of the mollusca, the representatives of the outer portion of the originally cellular epidermis (are not therefore comparable to the "cuticula" of a plant), inasmuch as the latter may always, in their young state, be traced over them. It is for this reason, I imagine, that they are at present ordinarily called "dermal" organs. A truly dermal or enderonic organ, however, ought, if it continues to grow, to retain the same characters as the enderon of which it forms a part. It ought, therefore, to have its protomorphic surface external and to grow exogenously. Now, no scale or plate of any fish, so far as I am aware, does this; on the other hand, it holds good of all, whether Placoid, Ganoid, Cycloid or Ctenoid*, that they commence by the occurrence of a calcfiic deposit immediately beneath the cellular ecderon, and that they increase by continual addition to the inner surface of this primary deposit. There are two ways in which we may conceive that these scales and plates are produced. Either they are a gradual calcification of the whole enderon from without inwards (which is the view taken by Leydig, of the scales of Polypterus), in which case the only tissue of the enderon capable of increase (that of the protomorphic line) being arrested by the calcareous deposit, the whole enderon at these parts must cease to grow, which would appear to be contrary to fact; or the scale corresponds with the cork-layer of the vegetable integument, and like it, though developed beneath the ordinary cellular epidermis, is still a truly ecderonic structure.

A great deal might be said for both these views; and if in this place, I assume the latter to be more correct, it is because I think we must be guided by the homology of the scales with certain other organs, where these relations are more definitely expressed. It may be taken as certain, I think, that the scales, plates, and spines of all fishes are homologous organs; nor as less so that the tegumentary spines of the Plagiostomes are homologous with their

* And I believe it will be found to be equally true of the "dermal" bones of reptiles and mammals.

teeth, and thence with the teeth of all vertebrata. Again, it appears to me indubitable that the teeth and the hairs are homologous organs; they are therefore either both enderonic or both ecderonic. Taking for granted the validity of a basement membrane as a mark of the boundary between ecderon and enderon, I elsewhere* arrived at the conclusion that the teeth are enderonic organs, and that therefore the hairs must follow them. Now, however, that a "basement membrane" turns out to be no test at all, there seems no reason why we should not be guided entirely by the direction of growth, and consider both hairs and teeth as ecderonic organs; the former being a development of the cellular ecderon, and corresponding with the ordinary horny epidermis; the latter, a development of a deep layer of the ecderon beneath this. It appears to me that we can do no other than admit this view for the teeth; but if this be the case, we may apply it to the scales of fish (and the "dermal plates" of reptiles?) also; as there are no difficulties about the latter which are not also presented by the teeth.

There appear, in fact, to be but few objections of any importance to the assumption of the ecderonic nature of fish scales, the principal ones being the continuation of the tissue of the ecderon over the upper surface of the scales; the apparent passage of the bony structure into the laminæ of the connective tissue of the enderon below, and the vascularity of the latter.

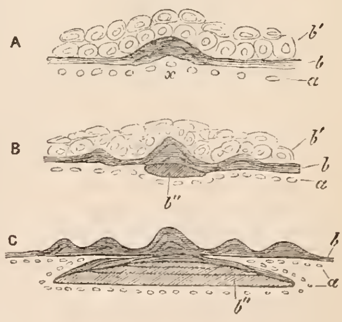
The continuity of the enderon over the scales will be seen below to be more apparent than real. I have not been able entirely to satisfy myself, as to the exact relations of the parts, in the case of the eel, but in the other fishes which I have examined the surface of the scale is very partially covered by the enderon, being in its centre, at any rate, in contact with the cellular ecderon.

The vascularity of the scale never extends to its most superficial layers, and may be explained in the same way as that of the test of an Ascidian, which however is unquestionably an ecderonic structure. The passage of its deep layers directly into the connective bundles of the enderon, which Leydig has observed in Polypterus (and which I will not say does not occur elsewhere, though I have not observed it), would appear to me only to indicate that this scale, and perhaps others, are composed of two portions, a superficial ecderonic part extending as far as the most superficial vascular canals, and a deep portion beneath these belonging to the enderon.

However, all these points can only be decided by a much more extensive series of investigations, principally directed to the ascertainment of the position of the protomorphic line and of the direction of growth of the constituents of every scale, than I have hitherto had time or opportunity to carry out; and as the attention of other observers does not appear to have been directed to these particular points, the question must for the present remain undecided.

Professor Williamson in his valuable and philosophical contributions to our knowledge of this subject (Phil. Trans. 1849-1852) laid the foundation for a comprehension of the mode of development of fish-scales, by pointing out that Agassiz's views, though essentially true, yet require a certain modification. For though a fish-scale does really grow by the apposition of layers to its deep surface, as Agassiz asserted, yet it is not included in a sac of the epidermis (if by that term we are to understand the ordinary cellular ecderon); and it is also true that its deeper portions grow by their superficial surface. Professor Williamson points out, in fact, that every fish-scale consists of at least two portions, a superficial homogeneous, or at most canaliculated, laminated layer, the *ganoin* (so called enamel or horny layer of authors), and a deeper, also laminated, frequently fibrous or osseous portion commonly traversed by Haversian canals. Now these two portions have a certain independence in their mode of growth, at any rate after their first formation, as may be easily understood by the accompanying diagram (*fig.* 307.), which represents a series of imaginary sections of scales from their first growth onwards; *a*, is the protomorphic plane; *b*, *b''*, the deep ecderon; *b'*, the superficial cellular ecderon, and the line *x*, the centre of the scales from which development commenced.

Fig. 307.



Suppose A to be the youngest scale, constituted merely by a thickening and calcification of the deep ecderon, which in B has added several layers by apposition to its inner surface, all of which retain the ganoin structure except the deepest, which becomes fibrous in its texture, and forms the commencement of the "Lepidine" layers of the scale;—these layers, however, being as much a part of the ecderon as the former. In C the scale widening, the edges of its "Lepidine" layer do not remain in contact with the ganoin layer; but it will be obvious that the re-entering angle thus formed by the protomorphic line between the two, is only, as it were, a fold of the deep surface. If the two layers go on increasing

* On the Structure and Development of the Teeth, Quarterly Journal of Micros. Science, 1852.

in this way, however, the ultimate effect will be that, although growing in reality by its deep surface as before, the "Lepidine" layer of the scale will appear to grow by its superficial surface, and that addition of layers to the upper surface of the scale observed by Professor Williamson, will take place. If the explanation here proposed, however, be correct, this will form no objection to, but a confirmation of, Agassiz' views.

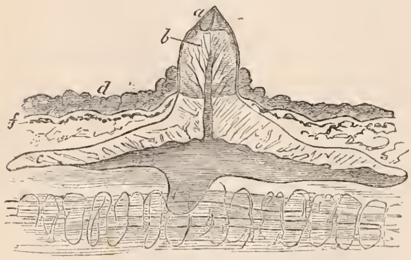
It will be well, however, with this clue to turn from the theory to the facts of scale development.

All that I have observed leads me to confirm Professor Williamson's conclusion, that there is no real line of demarcation to be drawn between placoid, ganoid, ctenoid, and cycloid scales; all these forms passing into one another. Indeed, I conceive that the only method thoroughly to comprehend the cycloid and ctenoid scales is to examine, in the first place, the so-called placoid and ganoid forms.

Hermann Mayer and Leydig have shown (and the fact is readily verifiable) that the scales and spines of the Plagiostome fishes are formed by the gradual deposit of calcareous matter in processes of the integument, which are at first coated by the ordinary cellular ecderon. These diverticula, in fact, originally resemble other papillæ of the skin, and like them, are bounded by a structureless protomorphic layer, marking the boundary between the cellular ecderon and the enderon.

When the formation of the placoid scale commences, however, instead of the successive division and multiplication of the endoplasts and the cellulation of the periplast of the ecderon, which before went on, a deposit of calcareous matter takes place at the boundary-line, and the structureless band remains as structureless or "basement" membrane, investing the future spine. The deposit increases until the enderonic pulp occupies but a very small space, or even completely disappears, and the spine projects as a cylindrical or conical tubercle. When it has attained its full length, the deposit does not cease; new calcareous matter is continually added to its inner extremity, but rather in the direction of breadth than of length, so that, eventually, an irregular broad plate is formed with the spine projecting from its outer surface (*fig.* 308.).

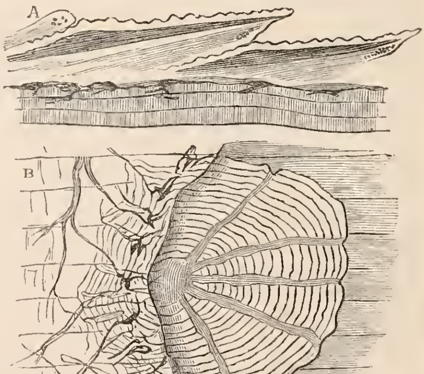
Fig. 308.



It is particularly to be remarked, however, that the projecting body of the spine being once formed, the calcareous additions which give origin to its base (*c*) gradually cease to be in exact apposition with the original protomorphic zone; and in proportion as the base of the spine extends, have we a wider and wider interval, occupied by the tissue of the enderon, between its upper surface and the under surface of the ecderon (*f*). Examining it in the perfect state, then, it would appear that the spine is included in a sac of the enderon; and this appearance is very much strengthened if dilute hydrochloric acid be added, by which the enamel layer (*a*) is dissolved out, and the structureless membrane enclosing the spine rendered distinct; while its continuity with that structureless layer which bounds the enderon is at once obvious. From its development, however, it is clear that this is a simple appearance, and that the apparent sac results from the projection inwards of the extremity of this truly ecderonic structure. In fact, inasmuch as the base of the spine grows like its shaft by continual addition to its inner surface, while its apex is unquestionably an ecderonic structure, this base might be considered to be enveloped in an involution of the protomorphic plane of the ecderon (*fig.* 307. c).

Now suppose such plates as these to have acquired their maximum in width and minimum in height; furthermore, imagine them to be so closely set in the skin that the posterior edge of one over-rides the anterior edge of the one next behind it, and we have the exact arrangement of the scales in the cycloid and ctenoid fish (*fig.* 309.).*

Fig. 309.



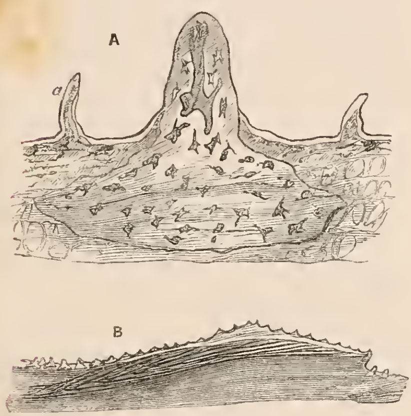
Scale of the Roach (*Leuciscus.*)
A, section; B, surface.

* The flexible cycloid scale of the eel presents an exact parallel to the tooth-like placoid scale of the skate, except that it is flat instead of conical, and that, in the adult state, the scale appears to be completely included in the enderon, and is wholly covered by the cellular ecderon. I believe this appearance of inclusion in a complete sac to proceed simply from the smallness of the original point of contact of the scale with the cellular ecderon, and the rudimentary state in which the whole organ remains.

A careful study of the scales of that remarkable animal the Sturgeon, which exhibits in this, as in so many other characters, its intermediate position between Teleostian and Plagiostome fishes, appears to me to throw still further light upon the difficulties of scale development.

The scales of the sturgeon are large, slightly convex, rhomboidal plates, set obliquely in the skin, so that, while the posterior two-thirds of their surface are bare and hard, the anterior third becomes gradually softer from the prolongation of the integument over it. The posterior surface continues hard up to its sharp edge, but it is supported below by a soft thick layer of integument, which passes on to the anterior soft coat of the scale behind, and thus masks the real overlapping of this scale by the posterior edge of that which precedes it (*fig.* 310. B).

Fig. 310.



Scale of Sturgeon.

A, one of the detached tubercles highly magnified; B, the entire scale.

The surface of the scale is shining and glassy. It is marked by a median ridge, whence it shelves upon each side, and by an elegant sculpturing produced by raised, hard ridges of the same nature, which radiate from the margins centrally, for about a fourth of the semi-diameter of the scale. In the region within this zone, the ridges gradually lose their regularity, the radiating lines anastomosing with one another and forming an elegant polygonal network. The soft surface of the integument of the anterior portion of the scale, is raised into many minute papillæ (*fig.*310. A, *a*), which may be followed for some distance on to the hard portion. Furthermore, it exhibits scattered round spots, with projecting centres of the same appearance as the ridges, and like them feeling hard to the touch.

If a section of the scale be made (*fig.* 310. B), its under surface will be found to have a concavity corresponding with the convexity of the upper. If the section has passed through one of the ridges, it is seen that the osseous tissue of the scale is of two kinds; a superficial homogeneous-looking, dense, comparatively thin layer, and a deep, thick, laminated portion. If traced from the centre of the scale to its anterior circumference the superficial layer loses its continuity, breaking up into conical bodies, which are the sections of the detached calcareous spots mentioned above; the deep layer thins out, its laminæ gradually becoming fewer, and leaving a soft membranous space between their upper surface and the under surface of these spots. In the centre of the scale again, a series of rounded apertures are seen in a tangential section, the sections of canals which radiate through the scale and become more numerous and wider towards its margin. They are connected below with vertical canals passing through the laminated layer, and anteriorly they pass into the wide membranous space above referred to. There is no histological difference of any importance in the structure of these two layers; each is composed of true bone with radiated corpuscles; the upper being more dense and homogeneous, the lower less dense and laminated.

If a section be made through several of the ridges of the upper surface, it will be seen that they are entirely composed of the hard homogeneous osseous tissue. On their sides, however, and in the valleys between them, more or less of soft integument remains, whose pigment masses give the valleys a dotted appearance. On the other hand, a section of one of the detached tubercles shows, except in its consisting of osseous tissue only, that it is identical with a single spine of the Skate (*fig.* 310. A). It appears to me, therefore, that there can be no doubt that the ganoid, overlapping scale of the sturgeon commences by an isolated placoid spine; that other spines are developed around this, and their bases uniting, constitute a placoid scale, between whose elevations little valleys, bridged over by the soft integument, remain; that to the base of such a plate as this, continual additions of osseous laminæ are made, the radiating Haversian canals being left between the first laminæ and the superficial plate; and finally that, extending in size, the anterior face of this complex scale becomes over-ridden by the preceding one. Complicated as it may appear, it is obvious that all this structure results from the continued endogenous growth and union of the primary ecderonic calcareous deposits, which constitute, as it were, so many centres of ossification for the large scale. The final structure, however, is (if we leave out of consideration its histological character), to all intents and purposes, that of a cycloid scale; and its mode of growth is identical with that of the large cycloid scale described by Prof. Williamson.

The increase of the scale is concentric; addition being made to its posterior, as well as to its anterior edge and surface; the only difference being, that in the latter case the development of the upper layer is less rapid than that of the lower, while in the former they are coincident; that soft membranous separation therefore, which exists between the two layers anteriorly, is far less developed posteriorly; and the soft continuation of the scale which is flat anteriorly, is inflected posteriorly; the process of addition being otherwise the same. Suppose, now, that each detached calcareous centre of ossification as it is added to the posterior margin of the scale, instead of being flattened, were produced into a spine as in the Rays, then it is perfectly clear that instead of a cycloid scale, the result would be a serrated ctenoid scale. And this appears to be exactly what takes place in the scales of the perch, according to Prof. Williamson's description.

From all this, I think, we arrive at Prof. Williamson's conclusion, that fish-scales are essentially tegumentary teeth; that like the latter organs, they result not from the calcification of the cellular ecderon covering those folds of the integument, upon which they are developed and which correspond with the dental pulp, but by a calcareous deposit taking place beneath this, in what represents a deep layer of the ecderon; finally that it is, for the present, an open question whether the deep layers of all scales are produced by a continuation of this process, or whether in some cases a deep truly enderonic structure may be added to this superficial ecderonic constituent to constitute the perfect scale. A process of the latter kind would, at any rate, find its parallel in the eventual union of the teeth of many fishes with their jaws, and in that of the plates of the chelonia with the vertebral elements.

§ 3. *Histology of the tegumentary organs.* — Having thus arrived at a general idea of the mode in which the various forms of integumentary organs are produced from the primary morphological constituents of every integument, we have now to consider their minute histological elements and the mode in which these proceed from the indifferent tissue of which all organs are primarily composed.

The tegumentary tissues, like all others, are produced by the metamorphosis of the periplast of the protomorphic or indifferent tissue from which they take their origin, the endoplasts, to all appearance, taking but little share in the metamorphic processes. The chemical metamorphosis of the periplast may be either into horny, chitinous, calcareous, or cellulose matter; in form it may become fibrous, laminated, vacuolated, bony, prismatic, &c.

As a general rule, the endoplasts tend to disappear, *pari passu*, with the metamorphosis in form and composition of the periplast; but the differences presented by different tissues in this respect have given rise to the establishment of a distinction between what is called the process of *conversion* and that of *excretion*. For instance, in the development of a hair or of a nail, the elements of the protomorphic layer evidently pass, as such, into the perfect substance of these organs; the periplast simply becoming horny, and the endoplasts remaining for a long while, or even always, visible in the cornified tissue. This is therefore a process of "*conversion*" of the protomorphic tissue. On the other hand, the chitinous coat of the lower Annulosa and the shells of the lamellibranchiate and gasteropod Mollusks arise in a totally different manner. The elements of the protomorphic layer do not pass into them entire, but they are formed, like the cuticula of a plant, or like the dentine and enamel of the teeth, by the successive outgrowth of layers of the outer portion of the periplast. No endoplasts, therefore, are ever found in them, and there is no *conversion* of the protomorphic tissue, but a process of *excretion*.*

At first sight this distinction would appear to be very decided, and likely to afford a good ground for the formation of definite subdivisions of the integumentary organs into classes. Unfortunately, it is often difficult in practice to assure oneself in what way a given tegumentary organ has been formed. While the presence of endoplasts in a metamorphosed tissue is good evidence of its having been developed by conversion, their absence is no proof that the tissue has been developed by excretion; inasmuch as it may simply be due to their very early disappearance. In fact, if any one affirm that the shell of a Unio or of a Crustacean, notwithstanding the impossibility of detecting endoplasts in its youngest laminæ, is in reality formed by the successive apposition of entire layers of the protomorphic tissue, in which the endoplasts disappear so early that they cannot be detected, it would be very difficult absolutely to disprove the assertion, though we might ask for evidence of its truth. Disbelieving in the doctrine of the special vital activity of the endoplasts, I confess the question does not seem to me to be of much importance, and I have only enlarged upon the subject because great weight has by high authorities been laid upon these distinctions. It appears to me that the processes of conversion and of excretion grade one into the other, and that no real subdivisions can be based upon the occurrence of either to the exclusion of the other. I will, however, take care to indicate what appear to me to be clear instances of each. I shall now proceed to consider the histological structure of the integuments of animals in the following order: — 1. Hydroid and Actinoid Polypes and Beroidæ. 2. Annulosa, including the Worms and Echinoderms. 3. Mollusca, including the Ascidians and Polyzoa. 4. Vertebrata.

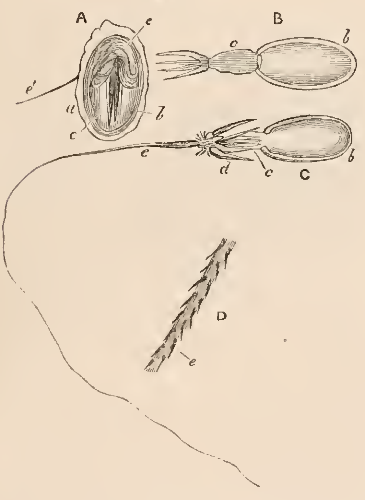
1. *Hydroid and Actinoid polypes.*—In these animals the integument consists either of a simple cellular and vacuolated ecderon, or the outer layer of this is developed into a structureless coat, which may become thickened by repeated additions, and thus attain considerable dimensions. In the common

* Using the word in the sense of "growth out," not in the common perverted signification of fluid transudation and hardening.

Campanularia, for instance, the outer wall of the bud from which a polype is to arise consists, at first, of a mass of indifferent tissue. As development proceeds, the outer portion of the mass is converted into a structureless membrane, which becomes detached from the body of the polype through its whole extent, and constitutes the future *cell*, the subjacent ecderon taking on the ordinary cellular structure. On the pedicle the same process goes on to a less extent, the structureless layer becoming separated only at intervals, so that the pedicle acquires a ringed appearance.

An integument of one or other of these descriptions is to be met with in all the Sertularian and Actinoid Polypes, and is obviously, in these cases, the result of a process of excretion. In the *Medusæ* and *Beroidæ*, on the other hand, where the integument is thick and gelatinous, the ecderonic tissue is converted, as a whole, into what closely resembles rudimentary connective tissue, in which elastic elements and muscular fibres are developed. The presence of peculiar organs, called the "*Thread or Urticating cells*," constitutes an extremely characteristic feature in the integument of these creatures. These

Fig. 311.



(*fig.* 311.) are composed of a delicate membranous sac (*a*), enclosing a much thicker one (*b*), which is open at one extremity, the aperture being stopped by the end of a more or less irregular short stiff sheath (*c*), sometimes giving attachment to several distinct rays or spines (*d*), applied together, which is fixed to the edges of the aperture, and occupies the axis of the inner sac. To the extremity of this sheath a long, frequently toothed filament is attached (*e*), and lies coiled up round the central sheath, and in close contact with the walls of the sac. The latter are very elastic, and seem to be tensely stretched by the contained fluid during life; for, on pressure, the sac suddenly bursts, and its contents are evacuated so rapidly as hardly to allow of the process being traced. I believe, however, that the long filament is pushed out by the side or through the axis of the central sheath, remaining still firmly attached to the latter, so that the result is the appearance exhibited in the accompanying figure (*c*), where the sac is seen empty, the long serrated filament being attached to the sheath, which, everted and with its spines spread out, is itself fixed to the margins of the aperture. The violent protrusions of these minute serrated filaments, aided, perhaps, by some aridity of the liquid of the sac, is in the larger kinds, such as those which exist in Physalia, exceedingly irritating to the human skin, and usually proves fatal to the minute creatures on which the Hydrozoic and Anthozoic polypes prey.

Integument of the Annulosa.—The integument of the lower Annulose tribes, of young forms and of the more delicate parts of a great majority of the higher Annulosa, consists of a thin structureless chitinous membrane developed from the subjacent cellular ecderon, in a manner essentially similar to what has been described in the Polypes.

Leydig has particularly described this form of integument in Entomostracous Crustaceans, (Branchipus and Argulus) in insect larvæ, (Corethra), and among the Annelids in Piscicola, Nephelis, Hæmopis, Sanguisuga, Clepsine and Lumbricus, where the integument consists of two portions—a deep cellular layer and a superficial layer, which is either absolutely structureless, or is fibrillated; being in no case formed by the coalescence of the subjacent cells, but by excretion from them.

A similar structureless excreted integument is found also in Planariæ, Nemertidæ, in many Cestoidia, Nematoidea and Trematoda, and, according to the late researches of Leydig, on Synapta, in the Echinoderms also. Where the integument is not very thin, and consists of several layers of chitinous matter, the added laminæ commonly take on a fibrous structure. The Nematoid worms present particularly good examples of this complication. Thus, for instance, the integument of Mermis albicans, which has lately been examined with much care by Dr. Meissner, consists of three layers, the middle of which is double. The outermost of these layers is either structureless or presents a distinction into transverse hexagonal plates, each of which occupies $\frac{1}{6}$ of the circumference of the animal. At the head and tail, small polygonal plate-like markings replace these, and such small plates could be detected, making up the large ones. Dr. Meissner calls them "cells," but expressly states that he never detected any nucleus in them, and it seems more probable that they are produced by modifications of the original external structureless layer, similar to those which, as will be seen, occur in the Crustacea and Mollusca.

The middle substance of this integument is composed of two layers of fibres one above the other. The fibres are parallel in the same layer, but those of the two layers cross one another at right angles, so that they form two sets of opposite spirals. The fibres are sharply contoured, dense, and brittle, and those of each layer are divided into six sets, corresponding with the six sections of the body. At the sutures the fibres of each bend back upon themselves, and run in a parallel course to the opposite suture.

The deep layer is the thickest; it appears longitudinally striated on section, and may be split into lamellæ of any thickness; otherwise it is perfectly structureless.

In the Nemertidæ, according to the researches of Quatrefages, the integument has essentially the same structure, consisting of a superficial structureless ciliated lamina, with deeper vacuolated and fibrillated layers. In the other Turbellaria the vacuolated structure is predominant.

This fibrous chitinous integument is still better developed in the Insecta.

According to Mayer (*l. c.*) the chitinous integument of Lucanus cervus is composed of glassy rods with sharply defined dark, parallel edges, which by their mutual apposition and anastomosis, and probably by the interposition of a connecting mass, form thin layers. The rods in each layer are parallel, but those of different layers cross one another at angles of from 45° to 90°; so that a horizontal section presents a sort of elegant cross-hatching, the lines of which are about 0·008 mm. apart. The outer surface of this laminated mass is invested by a transparent homogeneous substance containing pigment, and above this by a layer of epidermic "cells" (0·005 to 0·01 mm. in diameter), with nuclei and nucleoli, their edges being separated by an intermediate substance. Internally, there is also a layer of epidermic "cells" which are polygonal from mutual pressure. They are without nuclei, but possess a short spine, arising from the centre of the cell, and ending by a sharp point. Quekett (*l. c.*) describes a similar structure, consisting of striated laminæ, in the integument of Dynastes Hercules.

The integument thus described closely resembles that of the larger Crustacea (*vide infra*), and I should have placed it with them, except for the very distinct statement of Mr. Newport with regard to the development of the integument in Melöe. According to Mr. Newport's researches, the integument of the young Melöe is at first composed of polygonal nucleated cells, the largest of which is about $\frac{1}{2000}$ of an inch in diameter. As the animal grows, the nuclei divide and subdivide by a process of fission, and the integument becomes composed of several layers. After awhile, the deeper of these undergo a fibrous metamorphosis, and constitute a fibro-cellular structure, which gives attachment internally to the muscles, while the external layers continue to grow, and to be reproduced as distinct cells.

If this were the mode of development which obtained in all Insecta we must consider their chitinous integument to be produced by conversion of the previously existing cells of the ecderon. However, Leydig's statements are equally decided, that the integument of Corethra presents no appearance of cellular origin, and the question may, therefore, for the present, probably be considered undecided.

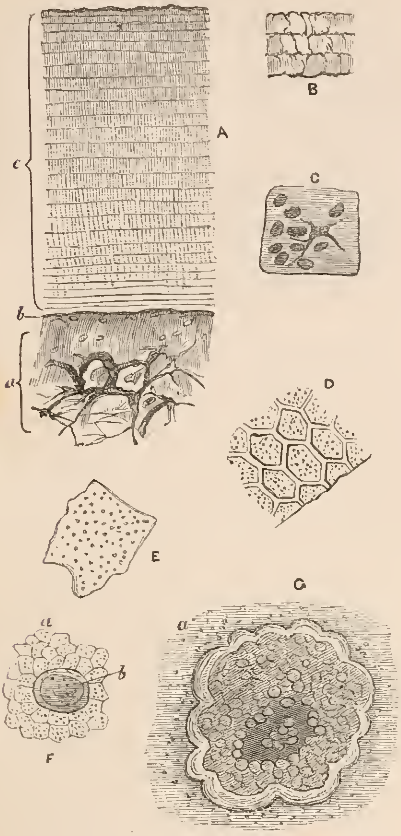
The calcified integument of the Crustacea presents the same general structure as that of the other Annulosa, consisting of superposed chitinous, more or less fibrous lamellæ, the outer of which are infiltrated with a calcareous deposit. In the small transparent Crustacea, as we have already seen, the integument is composed of structureless layers, developed by excretion on the surface of the ecderon, and even in the largest forms, the minute hairs, &c., present precisely the same appearance; but in the thick integument of the Decapoda, certain layers of the shell have been described, not without considerable show of reason, as possessing a cellular organisation (Carpenter).

I have carefully examined the shell of the common crab in relation to this point, and the following are the results of my investigation.

It appeared to me in the first place, that, without seeking for a moulting crab, the structure of the integument in its uncalcified state might be readily ascertained by examining the soft membrane connecting the articulations of the limbs, which, as is well known, is continuous on either hand with the calcareous integument, and passes into it. In a section of this soft layer (*fig.* 312. A), I found from within, outward, 1. The enderon (*a*) composed of connective tissue, excavated by vascular channels, and containing numerous aggregations of pink and yellow pigment, frequently disposed in a stellate form, or even forming anastomosing net-works along the rudimentary elastic fibres of the tissue. 2. The surface of this (*b*) was constituted by a protomorphic layer, consisting of a homogeneous substance containing endoplasts (C), which sometimes adhered to the enderon, sometimes to the hard integument, when the latter was detached. 3. Superficial to this, was the chitinous layer of the integument (*c*) composed of a number of laminæ of great delicacy, and not more than $\frac{1}{3000}$ of an inch apart. The deep laminæ were much softer than the superficial, and the outermost lamina of all was hardest, and of a brownish colour, constituting the structureless epidermis of Carpenter and Lavalle.

In section, the deep laminæ (B) presented only an indication of perpendicular fibrillation; but this became more marked superficially, the outer part of the section appearing closely striated. The deep laminæ, when stripped off, presented no definite structure, but they readily fell into plaits; while the superficial laminæ appeared dotted over. I sought in vain for any appearance of endoplasts in the deep layer, where, however, had they existed, they must have been readily detected; and I therefore conclude, that the chitinous lamellæ are formed from the subjacent ecderon, by a process of excretion. It should be remarked, however, that a minute polygonal areolation is observable at times upon the most superficial "epidermic" layer. I do not know from what cause this

Fig. 312.



A to E, from the crab; F, G, from the shrimp.

proceeds, but the areolæ are certainly not cells.

Such is the structure of the soft inter-articular integument, in which I could find no calcareous matter. If it be traced into the hard calcified shell, the only alteration observable is, that a dark calcareous deposit takes place, the earthy matter being infiltrated, as it were, through the laminæ. The deposit affects, however, only the middle layers, the extreme outermost being left as the "horny epiderm;" while a variable number of the inner laminæ remain as a more or less thick, soft coating upon the inner surface. These soft layers may be stripped off as a parchment-like membrane, with the muscles, and their relations to the enderon are then readily examined. They are here as structureless as where they constitute the deep layer of the inter-articular membranes.

The structure of the calcified layer has been carefully described by Dr. Carpenter, who showed, that in the crab and lobster they are traversed by tubules identical with those of dentine, and pointed out the error of Lavalle in regarding these as fibres. There can, I think, be no doubt, that in the crab and lobster, Dr. Carpenter's doctrine is correct; but I am equally of opinion, that for other crustacea, such as the shrimp, M. Lavalle is right. I believe, in fact, that the tubular structure is produced by the horizontal lamination giving way, as the calcareous matter is deposited, to perpendicular fibrillation of the chitinous matrix, and that, eventually, the uncalcified fibrils disappear, and leave tubules in their place. That at least appears to be a natural conclusion from the fact, that the perpendicular fibrillation of the soft tissue becomes more and more marked externally; and thus, by decalcifying the calcified shell, we obtain horizontal separable laminæ composed of short perpendicular fibres.

The colouring matter has always appeared to me to be generally diffused through the upper layer, and not to be confined to what Dr. Carpenter describes as the "cellular layer." The latter is a very thin stratum, made up of only a few of the superficial laminæ, which I have found to be most readily observable by detaching with a sharp knife a very thin scale from the upper surface of the crab shell. It is composed, exactly as Dr. Carpenter has figured it, of regularly polygonal, often six-sided areæ, frequently presenting a darker radiating patch in the centre, and, at first sight, irresistibly suggesting a true cellular structure.

I believe, however, that it is in reality nothing of the kind, but that, like similar appearances in the molluscan shell, this is simply the result of the concretionary manner in which the calcareous matter is deposited. We have seen, in fact, that there are no such appearances in the deep uncalcified layers, nor in the thin layers which invest the minute transparent appendages—considerations which appear to me to be in themselves decisive against the cellular nature of these bodies. In addition, decalcification brings to light no endoplasts in the "cells," but in their place we observe clear polygonal spaces in the membrane (*fig.* 312. D) which present the same dots (section of tubules) as those which exist in the simply laminated portion of the integument (*fig.* 312. E). Finally, if the decalcified scale include a sufficient number of layers, it is easy, by altering the focus of the microscope, to trace the areolation inwards, until it becomes gradually fainter, and disappears, passing into the ordinary dotted laminæ.

I believe, then, that the "cellular" layer, results from a peculiar additional deposit of calcareous matter in the uppermost layers of the shell; and this view is strikingly confirmed by what may be observed in the shrimp. The integument in this crustacean (*e. g.* the carapace) has exactly the same general structure as that of the crab, consisting of hard upper and soft deep layers, which are dotted and striated, and not tubular. The former owe their hardness to a generally diffused, transparent, calcareous deposit, which allows the previous dotted structure of the laminæ to be perfectly obvious. In some parts and in the superficial layers, this deposit is structureless and homogeneous (*fig.* 312. G, *a*), but in other parts the youngest layer presents very delicate polygonal meshes, whose areæ were about $\frac{1}{1000}$ in. in diameter (*fig.* 312. F, *a*). Decalcification completely destroys this appearance; so that I imagine it to be caused merely by the mode in which the primary deposit in the membrane takes place, the areolæ becoming almost immediately fused together by further deposit.

Through these homogeneous hardened outer layers thus constituted, there are dispersed more opaque spots (*fig.* 312. F, G, *b*), more or less rounded in their outline, and varying in diameter from $\frac{1}{500}$ in. or less, to ten times that size. The smallest of these bodies have exactly the appearance of cells (*fig.* 312. F, *b*), consisting of a dark centre, with a circular more transparent wall, and every variety of form may be observed between these and large masses, such as that figured (*fig.* 312. G, *b*), with a lobulated laminated circumference, and an irregular centre, composed of small masses like dentine globules. In the former the dots of the original tissue may be still seen; but in the latter they are not traceable and seem to be obliterated. If dilute hydrochloric acid be added while the object is still under the microscope, however, these bodies are gradually dissolved out with effervescence, and the structure of the place they occupied is found to be identical with that of the other portions of the integument. They are, therefore, nothing but concretions of calcareous matter, whose deposit has taken place in a peculiar form, quite independently of the primary structure of the part; this form being, in the smaller concretions, most deceptively cell-like. It appears to me that this case, in which the assumption of structure without cell development may be so plainly demonstrated, has a most important application, not only to the mode of formation of Crustacean and Molluscan shells (*vide infra*), but to the development of the teeth, strongly confirming, I think, the view which I have taken of that process.

Integument of the Mollusca.—The soft surface of the body of the Mollusca in general is constituted by an ordinary, commonly ciliated, cellular ecderon, which needs no special description. The hard or soft shells which so many of them possess, arise in two modes; the calcareous and horny integumentary appendages being, I believe, invariably produced by *excretion*, while the Ascidian test, which contains cellulose, is formed by *conversion*. It will be advisable to treat of the structure and histological development of these two forms separately; and, first, of the

Excretionary integument of the Mollusca.—This is to be met with in its simplest form in the Polyzoa, in which the integument (ectocyst of Allman) is formed by a structureless membrane containing imbedded calcareous or silicious particles.*

An admirable example of the calcareous integument formed by *excretion* is to be found in the shell of Unio and Anodon. The outer surface of the shell in these Lamellibranchs is, as is well known, covered by a brownish or greenish irregular membranous substance, the so called "epidermis" of the shell. This substance, however, by no means constitutes a single membrane; on the other hand, the surface of the shell is marked by an immense number of closely set, more or less parallel, concentric lines, some of which appear to be formed by rugæ of the "epiderm," while others are the free edges of epidermic laminæ cropping out under those of older date. Viewing this surface of the shell by transmitted light with a low power, a number of polygonal closely-set areæ come into view on depressing the focus through the thickness of the epiderm.

The inner surface of the shell has, for the greater part of its extent, a pearly or nacreous lustre; but along the gape of the shell, at a distance of from less than one line, to as much as two or three lines, from the free edge, the nacreous appearance ceases, and we find, instead, a brownish hue similar to that of the epiderm, and becoming gradually more intense till the very margin is constituted by a flexible brown membrane continuous and identical with the epiderm on the exterior. If the surface of the flexible zone be examined as before, its outermost portion appears quite homogeneous; as we pass gradually inwards, however, dots appear in it, and the hard portion of the brown zone presents polygonal areæ, precisely resembling those under the epiderm on the outer surface. Where the nacreous appearance commences, these areæ disappear, becoming obscured by an opaque white substance, which is marked by elevations and depressions, corresponding with, though less prominent than, the principal ones upon the external surface.

If, now, a section perpendicular to the surface and to the concentric lines be taken, and viewed in the same way by reflected light, the cause of the various appearances which have been described will become obvious.

It will be seen that the thick middle of the shell is composed of three substances; of a very thin external brown layer, the "epidermis," and of two other layers more or less equal in thickness; an external, composed of minute polygonal prisms or columns set perpendicularly to the surface, and an internal, which looks structureless, with a fracture like loaf sugar. The outer prismatic layer preserves its thickness as far as the "brown zone" above described, and then gradually thins out into the flexible marginal membrane. The inner nacreous layer, on the contrary, gradually thins out, and ceases at the commencement of the brown zone. The ends of the prisms are, therefore, bare in the brown

* I am indebted to Mr. Busk, whose extensive researches on these animals are well known, for the information on which this statement is based.

zone, whence the polygonal areolation observed in it; while its colour arises partly from the brown epidermis shining through, partly from a slight tinge of the same kind which runs through the prismatic substance, and renders it distinguishable, even to the naked eye, from the intensely white nacreous layer.

Thin vertical sections of these shells present the following appearances under a high magnifying power. The external edge is constituted by a delicate brown band, the "epidermis," in which no structure of any kind can be detected. Within this is the prismatic layer, a dense transparent substance marked by strong parallel lines which run perpendicularly to the surface and either extend completely through the layer, or terminate by joining some other within it. In the former case, the spaces which they enclose appear like the sections of prisms (of $\frac{1}{200}$ of an inch, more or less, in diameter): in the latter, they resemble longer or shorter cones whose bases are turned outwards. A number of such short cones are usually interposed between those ends of the prisms which are in contact with the epidermis.

Internally, or at the line of contact of the prismatic with the nacreous layer, the lines either remain parallel or converge.

The prisms are readily broken away from one another, and in this case, or in a sufficiently thin section of the whole layer, they are seen to be traversed by very closely set parallel transverse lines about $\frac{1}{10000}$ in. apart. Each prism, however, does not possess a set of striæ peculiar to itself; on the other hand, the parallel lines stretch without interruption through the whole length of the prismatic layer, as if the prisms were not there. A horizontal section of the prismatic layer presents, as has been said, a coarse polygonal reticulation corresponding with the lines of contact of the prisms. The substance of the latter appears granular, but without any other structure in fully formed portions (*fig.* 313. A).

When a section of the prismatic substance is acted upon by dilute acid, the calcareous matter is extracted, and a membranous framework is left, presenting all the structural characteristics of the original tissue, except that the prisms are now hollow, and from their transverse striations have been well compared by Dr. Carpenter to the scalariform ducts of plants. This membranous residuum readily tears up into laminæ, each of which corresponds, usually, to a number of the fine horizontal striæ.

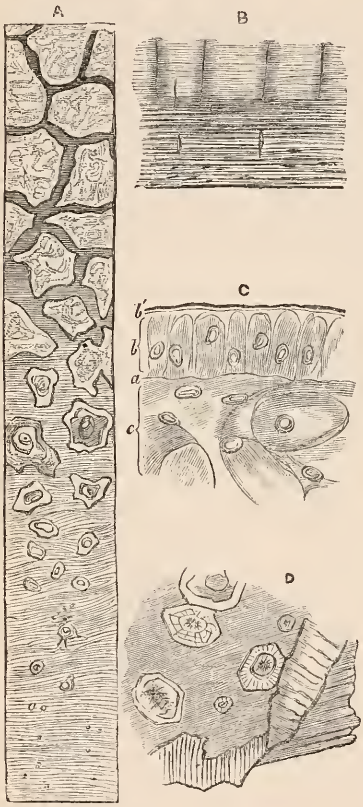
The white nacreous substance — *membraneous shell substance* of Dr. Carpenter—which constitutes the interior of the shell, presents, in a vertical section, a horizontally striated appearance identical with that of the prismatic layer, and when macerated in acid it breaks up into corresponding laminæ. In fact, if we leave out the vertical markings which give rise to the appearance of prisms in the latter, the two structures are identical. This point appears to me to have been overlooked and to have given rise to the impression that there is a much greater histological difference between the prismatic and membranous substances, than really exists. The examination of the line of junction of the two substances (*fig.* 313. B), however will at once show their fundamental identity. The ends of some of the prisms will be seen in fact to project beyond the others into the membranous substance; but it will be observed that the horizontal lines of the latter pass without interruption through the prisms, and therefore that the laminæ of the two structures are identical.

If we reduce these facts to their simplest expression, it will result that these shells are *composed throughout of superficial thin membranous laminæ, the outermost of which remains as epidermis, while the inner receive a deposit of calcareous salts.* Next comes the question, however, how are the structural differences between the prismatic and membranous layers produced.

Dr. Carpenter, in his well-known Essay, propounded the doctrine that both varieties of shell structure are the result of the development and coalescence of cells supplied by the mantle of the mollusk; these cells remaining permanently distinguishable and coalescing in rows, in the prismatic structure, but bursting and becoming confused into a homogeneous tissue, in the membranous substance. Nor, indeed, would it have been very easy in 1848 to arrive at any other conclusion than this, to which so great a number of appearances at first sight tend. Enabled, however, by Dr. Carpenter's great kindness and liberality to form my own judgment from his beautiful preparations, and having also worked over the fresh shells for myself, I have come to very different conclusions. I will not say that occasionally cells may not be enclosed in shell, but I believe I am in a position to show that, as a rule, shell-growth is not a case of *conversion*, but one of *excretion*, cells not being in any way directly concerned in the matter.

We may consider, first, the growth of the shell as a whole; and, secondly, that of its three constituents. Inasmuch as we know, that the shell of the young Unio or Anodon was once as thin as, or thinner than, the "epidermis" of the adult shell, and smaller than the smallest area, bounded by a concentric line on its outer surface; further, since we know that no addition is made to the outer surface of the shell directly; it is clear that the shell must grow in size by addition to its margin; in thickness, by addition to its under surface. Furthermore, since the extreme margin of any shell is constituted by the horny "epiderm," internal to which is the gradually thickening layer of prismatic substance, constituting the brown zone, within which again is the white nacreous area, formed by the superposition of membranous layers over the fully-formed thick prismatic substance; from all this, it appears to be equally certain that any given spot of the mantle of a young bivalve must give origin, directly or indirectly, first, to "epiderm;" secondly, to prismatic substance; and, thirdly, to nacreous substance; so that, on examining the free edge of a growing shell, we ought, since the "epiderm" is structureless and transparent, to be able to observe the gradual formation of the prismatic substance upon its under surface. This is, in fact, the case. *Fig.* 313, A, represents such a free edge of the shell of Anodon, *a* being the direction of the flexible zone; *b*, that of the perfect prismatic substance.

Fig. 313.



A to C, Unio; D, Helix.

Dr. Carpenter describes the appearances here figured in the following terms (*l. c.* p. 8.):

"Although the prismatic cellular structure has not yet been actually observed in process of formation, yet certain appearances, which are occasionally met with in the marginal portions of its newest layers, throw great light upon its mode of growth, and indicate its strong resemblance to cartilage in this respect; for in these situations we find the cells neither in contact with each other, nor polygonal in form, but separated by a greater or less amount of intercellular substance, and presenting a rounded, instead of an angular form (*fig.* 314. C). Upon looking still nearer the margin, the cells are seen to be yet smaller and more separated by intercellular substance, and not unfrequently we lose all trace of distinct cells, the intercellular substance presenting itself alone, but containing cytoblasts scattered through it. This appearance has been noticed by myself in *Pinna* and *Unio*, and by Mr. Bowerbank in *Ostrea;* so that I have no doubt that it is general in this situation. We may, I think, conclude from it that the cells of the prismatic cellular substance are developed, like those of cartilage, in the midst of an intercellular substance, which at first separates them from each other, that as they grow and draw into themselves the carbonate of lime poured out from the subjacent surface, they approach each other more and more nearly; and that, as they attain their full development, their sides press against each other, so that the cells acquire a polygonal form, and the intercellular substance disappears."

I have given Dr. Carpenter's statement at length, because it appears to me to express very distinctly the interpretation which one is at once tempted to put upon the appearance, but which I must reject for the following reasons:—In the first place, if we examine that portion (*a*) of the margin beyond the smallest granules (*cytoblasts*, Carpenter), it is seen to be either absolutely structureless or obscurely striated, not a trace of a cell or endoplast being anywhere visible. Secondly, if any dilute acid be added under the microscope, the apparent nuclei and cells vanish with effervescence, and leave behind them clear empty spaces, of exactly the same shape and size as they themselves had. Thirdly, the supposed cells have a peculiar concentrically or radially-striated structure, resembling sections of urinary calculi on a small scale, and still more the corresponding bodies in the integument of the shrimp (*suprà.*) For these reasons I think it must be granted that the appearances in question, however cell-like, are, in reality, not the expression of the development of a cellular structure at all, but merely that of the mode in which the deposit of calcareous matter takes place in the membranous basis of the shell. In fact, I believe that the calcareous matter appears first in small and distinct globules (the "cytoblasts"), and that more or less concentric deposits take place round these, the result of which is, that the membranous basis is more and more displaced, and that the deposited masses eventually come almost into contact. The regularity of the ultimate prismatic structure results from that of the distances of the granules primarily deposited, and the even rate of addition to each subsequently.

There appears to me to be but one interpretation to be placed upon these facts; viz. that cells as such do not enter into the formation of the shell of the Naiades at all, but that it is constituted by the successive excretion of membranous laminæ from the surface of the epidermis of the mantle.* The outer laminæ retain their membranous nature, only becoming so far altered as to assume the horny aspect of the so called "epidermis;" in the next laminæ, which are added to the inner surface of the young shell, calcareous matter is deposited in granules, additions to which are made in such a manner as to constitute the cellæform concretions, and ultimately, the process going on in the same way in successive layers, the prisms; in the innermost laminæ, finally, the calcareous deposit results in an even, homogeneous, folded or striated layer. By scraping with a sharp knife the inner surface of the shell of Anodon, freshly detached from the mantle, I have obtained a distinct tough membranous layer, scattered through which were a vast number of close-set irregular granules of calcareous matter. A similar structureless layer without the granules constitutes the outermost surface of the ecderon of the mantle (*fig.* 313. c, *b'*) and may occasionally be detached as such. Such a layer consisting of the thickened outer portion of the periplast of the ecderon of the mantle is by no means an anomalous structure, as we have a formation of exactly the same kind in the "cuticle" of plants, and in the chitinous lining of the intestine in Insects; and I believe that the shells of mollusks in general consist simply of a multitude of thin layers successively thrown off, super-imposed and coherent, all the peculiarities of their structure arising from subsequent modifications, which are altogether independent of cells. This view is in perfect agreement with all that is known of the nature of the shells of larval Gasteropods and Acephala, which are invariably either of an absolutely structureless, thin, transparent, membranous character, or at most present a delicate striation. It may be added that not the slightest trace of a cellular structure is to be met with in the pellucid shells of the Heteropoda and Pteropoda. So much for the two primary forms of shell structure, the membranous and the prismatic. A most interesting variety of the former is the *nacreous* (mother-of-pearl) lining which is presented by many shells, both of Acephala and Cephalophora. The pearly iridescence proceeds, as Dr. Carpenter has well shown, from the folding of the membranous layer into close plaits, and not, as has been supposed, from the alternate cropping out of calcareous and membranous layers. Dr. Carpenter proved this by decalcifying with acid a layer of nacre from *Haliotis splendens*. The iridescence remained; but if the plaits of the layer were pulled out by stretching it with needles, the iridescence disappeared.

Another variety of structure usually, but not alone found in the membranous shell substance, is the *tubular*. "All the different forms of membranous shell structure are occasionally traversed by tubes which seem to commence from the inner surface of the shell, and to be distributed to its several layers. These tubes vary in size from about the $\frac{1}{20000}$ to the $\frac{1}{2000}$ of an inch, but their general diameter in the shells in which they most abound is about $\frac{1}{4500}$ of an inch. The direction and distribution of these tubes are extremely various in different shells; in general, when they exist in considerable numbers, they form a network which spreads itself out in each layer nearly parallel to its surface, so that a large part of it comes into focus at the same time in a section which passes in the plane of the lamina. From this network some branches proceed towards the nearer side of the section as if to join the network of another layer, whilst others dip downwards, as if for a similar purpose" (Carpenter, *l. c.* p. 14.). In other instances the tubes run obliquely through all the layers. The former structure was found by Dr. Carpenter in the outer yellow layer of *Anomia ephippium*; the outer layer of *Lima scabra* and in *Chama*, the latter in *Arca*, *Pectunculus*, and *Trigonia*. In the latter case, the tubules are not continuous, but are seen under a high power to be formed by rows of isolated vacuities, one for each lamina; corresponding, I imagine, with the appearance, "as if they had arisen from the coalescence of lineally arranged cells," pointed out by Mr. Bowerbank and Dr. Carpenter. Having already given what are, I believe, sufficient reasons for denying the existence of cells of any kind in molluscan shells, I need hardly add that I cannot think this to be the true explanation of the mode of development of these tubules. In fact, I consider that the tubular shell structure is identical with that of dentine, and has precisely the same origin; its tubuli arising not from cells, but like the canaliculi of bone, by a process of vacuolation in the calcified tissue. I regard the structure and mode of development of the Molluscan like that of the Annulose shell, in fact, as evidence of the strongest and most unmistakable kind in favour of the views with regard to the formation of dentine which I ventured to put forth in my essay "On the Development of the Teeth." Tooth and shell completely represent one another, structure for structure; Nasmyth's membrane is the homologue of the "epidermis," the enamel that of the prismatic structure, the dentine, that of the membranous structure; and all three are produced without the intervention of cells by the differentiation of primarily structureless laminæ. The existence of tubuli in the prismatic substance is not mentioned by Dr. Carpenter, but I have noticed them very distinctly in one of the sections of Pinna from his cabinet.

Finally in Rudistes and the sessile Cirrhopods, Dr. Carpenter has pointed out the existence of a peculiar *cancellated* structure "like that of Pinna on a large scale" only that the segments of the prisms are hollow instead of solid. These hollow prisms are

* This is, after all, only a return to the opinion of Poli, whose observations on shell structure are remarkably accurate, and should never be overlooked. See his Testacea utriusque Siciliæ. Pars prima "in qua de Testarum natura atque affectionibus disputatur."

covered externally and internally by a structureless layer.

To complete this view of the different varieties of shell structure, it may now be interesting to consider the mode in which they are combined in the shells of the various classes of the Mollusca. In the *Brachiopoda*, the calcareous shell is composed entirely of membranous laminæ, which are superimposed at a very acute angle with the surface of the shell, and are further remarkable for being thrown into sharp folds $\frac{1}{2000}$ to $\frac{1}{700}$ of an inch apart, perpendicular to their planes. In the great majority of the recent species again, all the layers of the shell but the outermost are perforated by canals ·0006 to ·0024 of an inch in diameter, each of which contains a cœcal process of the mantle, corresponding with those processes which we have seen into the cellulose tunic of the Ascidians; the shells of *Lingula* and *Orbicula* are composed of horny laminæ perforated by oblique tubuli like those of dentine (Carpenter, *l. c.*). The shells of those families of Lamellibranchs, in which the lobes of the mantle are more or less united, are similarly composed almost entirely of laminated membranous shell substance, *e. g. Mytilus, Modiolus, Tridacne, Isocardia, Conchaceæ, Nymphaceæ.*

The tubular structure is met with in the *Arcaceæ*, in *Lithodomus*, in *Cardium*, and has generally a marked relation with the costations or sculpturing of the outer surface; the membranous and prismatic structures are combined in the *Myaceæ* and *Solenaceæ*, and in those genera which have the lobes of the mantle disunited, as *Ostrea, Unio, Pinna.*

In the Gasteropoda the shell substance is invariably membranous, but the laminæ of which the shell is composed, usually three in number, are marked by parallel lines into rhomboidal bodies, which are described by Dr. Gray as crystals, by Messrs. Bowerbank and Carpenter as elongated, mutually adherent cells. I believe that neither of these expressions is exactly correct, but that these bodies have the same origin as the prisms of the lamellibranchiate shell; a conviction in which I am strengthened by finding concentrically laminated bodies, like those of the Lamellibranchiates, upon the inner surface of the shell of *Helix* (*fig.* 313. D).

In *Patella* the middle layer is composed of perpendicular prisms, like those of Pinna. *Chiton* resembles it in this respect, but the outer layer is here composed of fibres parallel to the surface, and is pierced by short canals. In *Haliotis*, calcified plaited laminæ alternate with structureless horny layers, in immediate contact with which, says Dr. Carpenter, "is a thin layer of large cells of a very peculiar aspect." Dr. Carpenter considers that the plaited laminæ are cellular in this shell also.

Among the external shells of the Cephalopoda that of *Nautilus* has an external "cellular" layer as in Mya, and an internal nacreous layer like that of Haliotis.

The shells of all Lamellibranchiata, Brachiopoda, and of the majority of Gasteropod Cephalophora are external, being from their very origin never included in any involution of the mantle. It is different, however, with certain Cephalopoda and pulmonate Cephalophora, in which the shell commences its development as an internal organ covered over by the outermost layer of the mantle, and may either remain so enclosed during life (*e.g.* Sepia, Limax), or ultimately become naked as in Spirula and Clausilia. Although, however, these shells are truly internal (a distinction which, as I have endeavoured to show, carries with it some important conclusions),* yet the careful observations upon their development in Sepia by Kölliker, and in Clausilia by Gegenbaur, appear to furnish abundant evidence that they are still truly ecderonic structures, and that they bear the same relation to ordinary shell as a nail bears to a horny epidermis among the higher animals. We know, in fact, that the nail, though to all intents and purposes mere cornified epidermis, is at first an internal structure, being covered over by the outer layers of the fœtal epiderm. A nail remaining so covered would correspond with the shell of Limax or Sepia, while an ordinary nail represents that of Clausilia. Gegenbaur, in fact, has shown that the shell of the latter mollusk commences at first like that of Limax by the deposition of a layer of calcareous particles in the midst of the cellular ecderon of the mantle beneath its outer layer of cells. The shell of Limax goes no further than this stage, while in Clausilia (and probably in Helix, &c.) it gradually increases by addition to its under surface, and finally bursts through the cellular investment which takes no share in its formation. It is the same with Sepia. Here the internal shell, or sepiostaire, is composed of two layers, a dorsal and a ventral; the former, according to Kölliker, is a thin membrane composed of slightly wavy, parallel, somewhat dark fibrils 0·001–2″ broad, which frequently appear to be composed of still more delicate fibrillæ. So far as this membrane corresponds with the ventral layer, it is covered on both surfaces by a thin structureless lamina of carbonate of lime, which has a pearly aspect on the ventral surface where it is not covered by the ventral layer; while it is granular on the dorsal surface, and on the ventral, where it is covered by the proper ventral layer, presents ridges to which the plates of the latter are attached. The thick ventral layer of the sepiostaire is composed of lamellæ set at a very oblique angle to the dorsal layer, and united together by close-set partitions at right angles to their surface. Acted upon by acid, this portion of the shell leaves behind it a membranous skeleton of exactly the same form, but presenting no further structure.

Young embryos present merely a fibrous rudiment of the dorsal layer. The ventral

* See Memoir on the Morphology of the Cephalous Mollusca, Phil. Trans. 1852.

layer is formed by the successive deposit of calcareous laminæ inwards. When the first lamina has been formed, a deposition of small cylindrical bodies takes place upon its inner surface. These increase, widen and become ramified at their extremities, forming ramified columns. A second calcareous lamina is now formed, connecting their ramified extremities, upon whose under surface the like process takes place, and this is repeated until the ventral layer has attained its full thickness. The ramified columns are regularly transversely striated; with the age of the shell additions are continually made to their lateral dimensions until they coalesce and constitute the septa of the perfect shell, upon which the striæ remain visible.

Kölliker was unable to find any cellular structure in the columns or laminæ themselves, but describes a layer of nucleated cells under the shell, which he regards as the agents in its secretion. Some researches recently made by H. Müller (Gegenbaur, Kölliker and H. Müller, *l. c.*) corroborate this view. He finds the shell of the Loligidæ invested by an excessively vascular membrane, which is almost wholly covered by a layer of epithelial cells towards the shell. On the dorsal surface they are for the most part rounded ; on the abdominal surface, and particularly towards the anterior point, they form narrow cylinders which attain a length of as much as 0·07‴. They appear to give rise to the structureless layers of the shell. The lateral styles of the Octopods present similar relations.

The structure thus described, though apparently so widely different from that of ordinary mollusks, does not really differ very widely from the cancellated shell structure of Rudistes, &c., or still better of Pleurorhynchus as described by Dr. Carpenter. If we leave out the sides of the hollow prisms in the latter shell in fact, it will correspond exactly with one lamella of the ventral layer of the sepiostaire.

For a comparison of the shells of Spirula and Belemnites with those of Sepia and of Gasteropods, I must refer to Dr. Carpenter's Memoir so often cited.

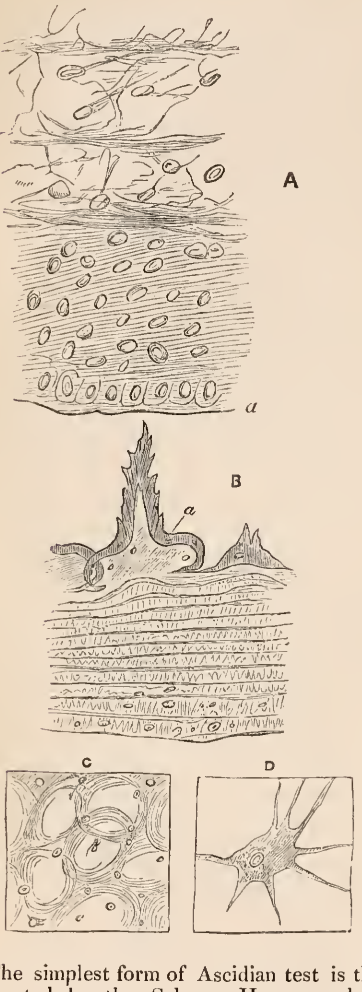
2. *Conversionary integument of the Mollusca containing cellulose.* — This form of integument has hitherto been found in the Ascidians alone, in which the existence of cellulose was first detected by Schmidt in 1845. Schmidt's discovery was confirmed, the fact of the existence of cellulose in all the genera of Ascidians determined, and the chief morphological characters of their test set forth in the memoirs by Löwig and Kölliker " Sur les Enveloppes des Tuniciers," which appeared in 1846, since when further investigations have been made by Schacht and by myself. I must refer the reader to these papers for an account of the various opinions which have been entertained with regard to the structure of the Ascidian test, as I can only lay before him what are in my belief the facts of the case.

The test of the Ascidians is never composed of pure cellulose, but consists of an animal membranous matrix, to which the cellulose has the same relation as the calcareous salts have to the membranous basis of bone or of shell. The cellulose is, in fact, diffused through the membranous matrix, thoroughly impregnating it.

This membranous nitrogenous matrix in which the cellulose is deposited, presents great diversities of structure in the genera of Ascidians, representing, in fact, almost every known tissue. Thus in one genus we have a test resembling cartilage ; in another, like bone ; in a third, like connective tissue. It may either be without vessels or traversed by branched and ramified vascular processes of the body. It is in all cases, however, a product of the metamorphosis of the ecderon of the outer tunic or mantle and, complicated as its structure may be, corresponds morphologically with the shell of other mollusks, or with the epidermis of the higher animals. In fact, if a section be made through the outer tunic and test of an Ascidian, as in *fig.* 314. A, taking care not to disturb the natural relations of the parts, we observe at the line of contact between the outer tunic and the test (*a*) an arrangement of the parts very closely resembling what exists at the junction of the derma with the rete Malpighii in the human skin. The outer tunic, like the former, is constituted by bundles of rudimentary connective tissue which run inwards to form sheaths around the muscles, leaving between them spaces, the sinuses of the blood vascular system, while externally they fuse together into a homogeneous substance containing endoplasts, which is thrown into processes and passes insensibly outwards into a layer of similar substance, with very close-set endoplasts almost perpendicular to its surface, which forms the commencement of the proper test. Externally to this rete Malpighii, the deposit of cellulose commences; the tissue undergoing at the same time a fibrous metamorphosis. The line *a* is therefore a protomorphic line, and the test is the product of the growth and *conversion*, by deposit of cellulose within its elements, of a true ecderon.

The separation of the ecderon (or test) from the enderon (outer tunic) takes place with great readiness in some Ascidians, as Phallusia, &c.; while in others, such as Boltenia, many Cynthiæ, Salpæ, &c., it can be effected with considerable difficulty, or not at all, and this difference has even been raised to the rank of a zoological distinction, the Ascidians having been in consequence divided into Monochitonida and Dichitonida. I believe, however, that in all those Ascidians whose test is unprovided with vessels, it is, normally, closely adherent to the outer tunic, and I am inclined to think that this is equally true even of those forms, such as the Phallusiæ, in which in preserved specimens the test and outer tunic are so commonly found detached from one another. Here, however, as the test is provided with an abundant vascular supply proceeding from one point of the body, it may normally become separated elsewhere. Careful examination of fresh specimens can alone decide this point.

Fig. 314.



The simplest form of Ascidian test is that presented by the Salpæ. Here, we have merely a gradual growth of the periplast and a deposit of cellulose within it, the endoplasts either remaining as such or becoming surrounded by cell walls. The resulting tissue, in fact, is identical with cartilage, if we suppose cellulose to have taken the place of chondrin.

In the Pyrosomata, the test has a structure which, on the one hand, resembles bone, on the other some forms of fibro-cartilage. The endoplasts, in fact, have become surrounded by cell walls, which are produced into long, frequently anastomosing processes (*fig.* 314. D); these retain their animal composition, while all the immediate tissue is strongly impregnated with cellulose. This is the fundamental structure of the test in the Phallusiæ and Clavelinæ also; but here an additional complication results from the development in the substance of the test of a series of rounded cavities, which gradually enlarge until they almost come into contact, and give rise to a spongy texture. The intervening septa at the same time frequently become obscurely fibrous (*fig.* 314. *c*). Now these "vacuolæ," whose origin and nature appear to me to show their identity with the "cancelli" of bone developed from cartilage, have been described by Löwig and Kölliker, and by Schacht as cells; and the latter has even stated that they possess a nitrogenous lining membrane. This is, however, a mistake, arising from the imperfect operation of the reagents by which the cellulose is detected; it is simply less abundant close to the cavities of the vacuolæ, but may with care be demonstrated to exist up to their very edges.

Botryllus, Synöicum, Syntethys, Boltenia, and the Cynthiæ, present a new series of appearances: here the periplast of the ecderon is metamorphosed into fibres, which, however, are not composed of pure cellulose, but of a nitrogenous substance impregnated therewith. In Synöicum the test is soft, and presents very much the structure of some forms of rudimentary connective tissue. We find, in fact, a more or less distinctly fibrillated basis with scattered endoplasts; some of these are invested by round granulous nitrogenous cell-walls, while in others the cells are spindle-shaped and prolonged at each end into fibres (representing thus the elastic element of ordinary connective tissue), or they may be stellate. Botryllus, Syntethys, and Boltenia, present a similar structure, varying, however, in the extent to which the nitrogenous cell-walls on the one hand, and the periplast impregnated with cellulose on the other, have undergone development. Thus the periplast is broken up into very obvious fibres in Botryllus, while in Boltenia the fibrillation is pale and indistinct. On the other hand, I have nowhere met with so great a development of the nitrogenous cell-wall as in Synöicum.

In Boltenia a more or less distinct lamination makes its appearance in the test, and this peculiarity, as well as the fibrous structure altogether, attains its maximum in the Cynthiæ. In Cynthia papillata, for instance, the middle substance of the test is composed of numerous, very obvious laminæ, which consist of fibres directed alternately parallel with, and perpendicular to, the surface of the test (314. B.) At first sight, they appear as Löwig and Kölliker have described them, to be decussating sets of longitudinal and radiating; but on a careful examination of their sections I invariably found that the apparently radiating fibres bend round as they approach the apparently longitudinal set, and in fact pass into the latter. The longitudinal bands are, however, no thicker at one end of a section than at the other, so that the transverse fibrils cannot be merely given off from them. A transverse section, again, exhibits the same appearances as a longitudinal one; so that I think the fibres must in reality have a more or less regularly circular arrangement around the centre of the spaces occupied by the radiating bands, the apparently longitudinally fibrous bands arising merely from the decussation of these circular fibres. Great numbers of granular corpuscles (endoplasts ?) are scattered through the midst of the "transversely fibrous" spaces. In Cynthia pomaria, Löwig and Kölliker describe peculiar "cells" in the inner layer of the test, consisting of such corpuscles surrounded by a thick circularly fibrous wall, and the existence of these bodies appears to be additional confirmation of the view I have taken as to the mode in which the fibres in Cynthia papillata are disposed. If in the latter, the fibres were disposed more closely around particular corpuscles, the test would, in fact, break up into just such circularly fibrous cells.

I have hitherto described only the structure of the middle, most characteristic portion of the Ascidian test; it is next necessary to notice the inner and outer surfaces; the former of which is ordinarily said to be covered by a cellular epithelium, the latter by a more or less structureless horny epidermic layer.

The so-called epithelium is, I believe, in all cases merely the innermost unmetamorphosed layer of the ecderon, corresponding with the rete Malpighii of the "epidermis" of higher animals. As the Ascidian integument is ordinarily examined (*i. e.* in spirit specimens), it is in the condition of the macerated integument of one of the higher animals, and just as the "epidermis" of the latter may or may not, if stripped off, bring away with it the deepest layers of the *rete*, so the Ascidian test, when detached from the outer tissue, may or may not retain the corresponding structure.

The horny so-called "epidermis," on the other hand, is a structure well worthy of attention, as a similar element is, as we have already seen, to be met with in the widely different integuments of other Mollusca. In all Ascidians I have found the outermost surface to be formed by a structureless homogeneous layer, which contains less cellulose than the subjacent tissue, and often has a brownish horny aspect. In many Salpæ, Phallusiæ, and Cynthiæ, this outer layer constitutes merely a tough wrinkled investment. In others (Synöicum, Boltenia) it is prolonged with the subjacent layer into spines and processes, but without being much thickened. In other Bolteniæ again, and in various Cynthiæ, it is greatly thickened, and almost by itself constitutes large spines or even tesselated plates. In Cynthia papillata (*fig.* 314. B), the whole outer surface of the test is covered with spines (*a*), whose bases expand into polygonal plates, which strongly resemble the spines of the Rajidæ, to which reference will be made below. The brown substance here appears to have invaded the subjacent tissue, leaving spaces for the pre-existing endoplasts, so as to give rise to a structure precisely resembling the bone of the Plagiostomes, while to complete the resemblance, the pointed extremity of the spine is marked by lines which pass from its central cavity, parallel with one another, to the surface. I am not sure that there are tubes, but otherwise the appearance is exactly that presented by the pseudo-dentine of the integumentary spines of the skate.

It would appear, according to Milne Edwards, and the late observations of Krohn, that the rudiment of the mantle exists in the ovum of Phallusia before the cleavage of the yolk commences, as a structureless pellucid coat, containing solitary or aggregated greenish cells; and it would seem as if the outer structureless layer with which we are at present concerned, arose from this coat, while the main thickness of the mantle is the product of the metamorphosis of the subsequently developed ecderon.

From all that has been said, I think it results that the Ascidian test is formed from the ecderon of the animal by a process of conversion which consists in the deposit, through its periplast, of cellulose, and a coincident morphological change which may result in the production of a tissue essentially resembling either cartilage, bone, connective tissue, or even dentine; and that, therefore, an attentive study of the integument in this class alone is sufficient evidence that mere structure is no proof of the ecderonic or enderonic nature of any given organ.

Integument of the Vertebrata. — In these animals there are two classes of integumentary organs, differing in structure, chemical composition, and mode of development. These are, 1st, the *horny* and *glandular* tegumentary organs produced by the *conversion* of the cellular ecderon; and 2nd, the *calcified* tegumentary organs which appear very frequently to be developed by a process of *excretion*.

1. *Conversionary horny organs.*—If a section be made of the integument of any mammal, it will be seen to be composed, leaving out of view its various appendages, of two principal portions, the enderon or derm, and the ecderon or epidermis. The latter, separated by a more or less distinct transparent line from the former, is internally composed of a homogeneous soft substance, in which are dispersed numerous oval or rounded endoplasts, set more or less perpendicularly to the surface of the enderon. Further outwards, they gradually become more distant and a cavity is developed round each, so that the ecderon becomes distinctly cellular. Still more externally the cellular periplast becomes changed in composition, being converted into a denser horny substance, and the change usually takes place so suddenly that the horny external portion (epidermis) is sharply marked off optically, and can be readily separated mechanically and chemically, from the internal unaltered soft portion, the *rete Malpighii.* The cell cavities at the same time become flattened, and by degrees almost obliterated, apparently by the pressure of the subjacent growing tissue; but the endoplasts remain, and may always be detected if the horny layers are

distended and rendered transparent, by the action of acids or alkalies. The horny stratum of the epidermis is therefore the result of the *conversion* of the walls or periplast of a whole layer of the cells of the ecderon into horn.

The hard structures of nails, hoofs, and horns (*i. e.* horny sheath of the horns of Ruminants) are developed in exactly the same manner; nor am I aware that any tissue enters into these organs, which is not entirely produced by the horny conversion of a cellular ecderon. The hoof of a fœtal lamb was entirely composed of such horny cells.

Structure of hairs, spines, and feathers. — In these tegumentary organs, we have to consider, first, their own proper structure, and, secondly, that of the sacs in which they are at first wholly, and always partially, enclosed.

The *shaft* of a hair is composed of three distinct structures, an external, the *cuticle;* a middle, the *cortex;* and an internal, the *medulla.*

Fig. 315.

Hair, Man.

A, B, D, E, F, from the nose; C, from the head.

The *cuticle* (*fig.* 315. C, D, E) on that portion of the shaft which lies within the hair sac, consists of two layers, while only the inner of them remains in the protruded portion. Viewed in section, as when a hair is observed in its totality, the cuticular layers form a thin double margin to the shaft, the outer (*b*) having the appearance of minute rhomboidal cells, joined end to end; the inner (*a*) seeming to be composed of close-set fibres arranged parallel to one another, and obliquely to the axis of the hair. If, however, the focus of the microscope be adjusted to the surface of the hair, or if the cuticular layer be detached from the shaft, these rhomboidal cells and parallel striæ are found to be the expression of irregular transparent structureless plates, overlapping one another, and closely united into tough membranes, to which their projecting edges give a striated appearance. No trace of endoplasts is visible in the older of these plates, and the matter of which they are composed is singularly unchangeable, remaining untouched on the addition of strong sulphuric acid, or of caustic potash, which completely dissolve the inner substance of the base of the shaft, and leave the cuticle in the form of a transparent, colourless, double membrane. In man, the outer layer of the cuticle ceases at the level of the sebaceous glands; and the edges of the plates of the inner layer lie very closely appressed to the shaft; in many of the lower animals, however, the plates are at a greater angle to the axis of the hair, and their projecting edges give rise to the most elegant sculpturings of its surface.

The *cuticle* proceeds from the horny metamorphosis of the two outermost layers of the pulp of the hair. The lowest portion of the bulb of a hair, if viewed in section, presents a sharply defined edge (*fig.* 315., C), which may occasionally be raised up by reagents as a distinct structureless membrane; but is normally perfectly continuous with the subjacent transparent homogeneous periplast of the pulp, in which lie the ordinary rounded or oval vesicular endoplasts of young indifferent tissue. Tracing the margin of the hair upwards, we find, next, that the two most superficial series of these endoplasts (D, *a*, *b*) are distinguished from the rest, by being free from that deposit of pigment granules which surrounds the endoplasts of the proper shaft substance; and these two series are more or less distinctly contained in cavities or cells. The outer series is disposed more parallel, the inner more perpendicular to the surface. Still higher, (E) the cavities of the outer series are larger, and their party walls straight and sharply defined, while the endoplasts, which were at first plainly visible, disappear. In the inner series, both cavities and endoplasts disappear, and the periplast seems to split up into thin parallel horny plates (E), whose edges become more and more strongly marked. Such are the steps in the development of the cuticular layers which may be observed in short thick human hairs, such as those of the nostril. In those of the head, however, and in the hairs of the body of the calf, I have been unable to trace the cuticle into anything but a structureless layer, wrinkled externally, which passed into the superficial structureless layer of the deepest part of the bulb (C). I formerly thought that this indicated an important difference, but it is readily accounted for, if we suppose the process of development to be the same in each case, the endoplasts only disappearing very early in the latter.

The main substance of the rest of the shaft of all hairs, and its entirety in some, is composed of the *cortical tissue.* This is a horny hard substance, clear and homogeneous in white hairs, but filled with pigment granules, and moreover having its own special coloration in coloured hairs, which may be broken up mechanically, or by the action of strong alkalies and acids, into long, pale, sometimes striated fibres, which may or may not present remains of elongated endoplasts. Besides the latter and the pigment granules, a multitude of striæ and dots are visible in the cortical substance, which are produced by canals and cavities containing air.

The cortical substance results from the metamorphosis of the corresponding portion of the hair bulb. The primarily rounded vesicular endoplasts (*fig.* 315. A), become greatly elongated and spindle-shaped, without ever, so far as I have been able to observe, becoming surrounded by a distinct cell cavity or wall (*fig.* 315, B). At the same time pigment granules arise in the periplast; it acquires a fibrous appearance, becomes horny, and splits up more and more readily into plates and fibres in the direction of its length. As it attains its perfect structure, rounded and elongated vacuolæ, which there is no reason whatever to suppose result from confluent cell cavities, arise in it and become filled with air. In fact, the perfect cortical substance is a sort of rudimentary horny dentine.

Lastly, the *medullary substance* — which attains a considerable development in the short thick hairs of man, and in those of the body of many mammals, but is frequently absent, as in the hair of the head of man, and according to Brücke (Reichert's "Bericht," 1849) in the bristles of the pig, the whiskers of the dog, seal, walrus and the long hairs of Myrmecophaga jubata—consists of a horny matter like that of the cortex and continuous with it, excavated into polygonal cavities, which frequently contain air bubbles and pigment granules. The cavities communicate, and the air may be driven from one into the other.* In the fully formed hair, they contain no remains of endoplasts. The medullary substance, like the cortical, proceeds from the metamorphosis of the indifferent tissue of the pulp, but the process, instead of being one of vacuolation and fibrillation, is essentially one of cellulation. The endoplasts, instead of elongating, remain rounded. Cavities are developed round them, whose partition walls become thick and granular. The cavities then gradually enlarging eventually open into one another, and the endoplasts disappear. The whole structure and mode of development of this tissue, in fact, show its complete identity with the "pith" of feathers, as we shall see more fully below.

The *hair sac* is an involution of the whole integument, and as such is composed of an enderonic and of an ecderonic portion. The former, which is continuous with the subcutaneous tissues, when well developed, consists externally of a network of fine elastic fibres, within which is a layer of homogeneous tissue containing endoplasts which are more or less elongated transversely, and which form the superficial layer of the enderon. Within this is a structureless layer, the commencement of the ecderon, enclosed by which are the representatives of the cellular ecderon, the so-

Fig. 316.

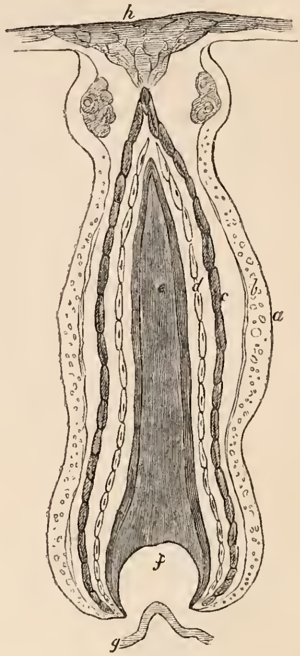


Diagram illustrative of the position of the different layers of the hair sac in a young hair.

a, *b*, outer rootsheath; *c*, fenestrated rootsheath; *d*, imperforate rootsheath.

called *rootsheaths*. These are commonly described as two, the *outer* (*a*) and the *inner* (*c*, *d*); the latter again being composed of two structures, an external, the *fenestrated inner rootsheath* of Henle, and an internal, which I described in 1845, and which may be called the *imperforate inner rootsheath*. The *outer rootsheath*, like the others, is thicker above than below, thinning out where it joins the bulb at the bottom of the sac. It consists entirely of tissue resembling that of the rete mucosum, and needs no particular description.

The *fenestrated, inner rootsheath* lies in immediate contact with the outer rootsheath. It is composed of more or less rounded or polygonal flat plates, with faintly marked boundaries, united by their narrow ends, and leaving spaces between their sides (*fig.* 315. F). It is very tough and resistant, both to mechanical and chemical action, and no endoplasts can be seen in its elements. The *imperforate rootsheath* (*a*) is composed of flat thin flexible plates not unlike those of the preceding layer; but they present no intervals, their boundaries are strongly marked, and in the centre of each there is a peculiar, elongated, often more or less dumb-bell-shaped endo-

* Griffith, Lond. Med. Gazette, 1848.

plast. In the human hair sac there are usually only one or two laminæ in this layer, but in Rodents there are said to be many.

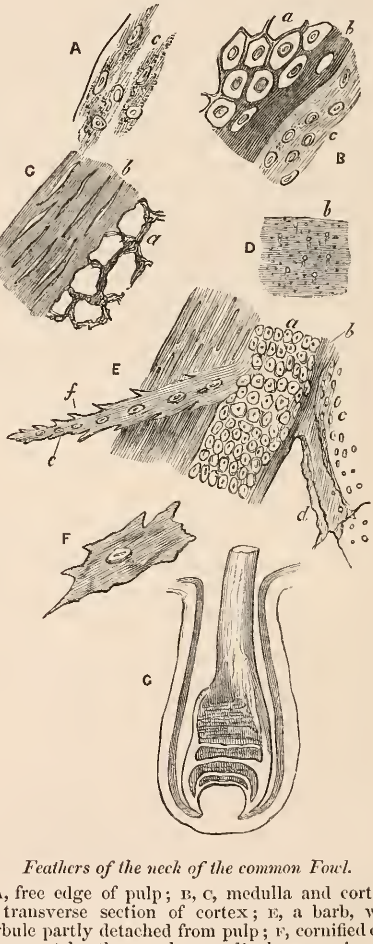
If we examine a hair sac above the level of the bulb, it will be clear that these inner rootsheaths are not generated from the contiguous surface of the external rootsheath, as would at first seem probable. No transitional forms, in fact, are visible in the direction of the transverse diameter of the sac. Traced towards the base of the sac, however, it is obvious that opposite the lower portion of the bulb the inner layers of the outer rootsheath become metamorphosed into horny cells; and that of these cells, the inner are converted into the imperforate layer, while the outer undergo a more complete cornification, and lose all trace of their primitive endoplasts. The clefts which ultimately exist between these cornified plates are not present in the young state, but are the results of a secondary vacuolation. They have nothing to do with the disappearance of the endoplasts; for traces of the latter may be observed in the *centre* of horny plates, at whose *edges* the clefts are commencing (*fig.* 315. F). It would appear, therefore, that the rootsheaths grow like the shaft of the hair itself, not by addition to their surface, but by growth of their deep-seated inner ends.

Such is the composition of the growing hair; but the completely formed hair (see § 2. *Morphology*) presents very great differences in the minute structure of its inner termination. In the first place, the shaft runs out into an irregularly conical mass, like a worn-out painter's brush. It consists, at its extremity, entirely of cortical substance, and the cornification runs in irregular lines into the indifferent tissue, which occupies the bottom of the hair sac and represents both pulp and outer rootsheath. The inner rootsheaths terminate above this point, in an irregularly horny layer, which unites with, and is in a manner reflected into, the cuticle of the shaft, which ceases above its brush-like expansion. Finally, the outer rootsheath in the immediate neighbourhood of the inner, is metamorphosed into large horny cells, like those of the cellular ecderon. The development of these from the indifferent tissue of the outer rootsheath, may be very clearly traced. The periplast first becomes enlarged and marked off into definite granular areæ around each endoplast, and the limits of each area are metamorphosed into clear horny walls. The cavity which these inclose enlarges, and the endoplast, with its surrounding granular matter, remains attached to one wall, and then eventually disappears, while the cavities enlarge, and their walls thicken into clear horny "cells," which may eventually be detached from one another.

The whole process of the completion of the root of a hair, then, is simply a return of the diverticulum of the ecderon, — the metamorphosis of whose elements, so long as the hair was in course of formation, was guided and determined into distinct forms along certain fixed lines, — to its general tendency to undergo the ordinary cellular metamorphosis over its whole surface. With this return to its primitive tendencies, the increase of the hair of course ceases, and sooner or later it is pushed out and falls away.

The spines of the Porcupine, of the Hedgehog, and of the Echidna*, present in their histological, as in their morphological relations, an interesting approximation to feathers. Externally, they are coated by a cuticle, while the principal mass of their walls consists, at the ends, of a fibrous horny substance; in the middle, there is added to this a medullary substance composed of polyhedral horny cells.

Fig. 317.



Feathers of the neck of the common Fowl.

A, free edge of pulp; B, C, medulla and cortex; D, transverse section of cortex; E, a barb, with barbule partly detached from pulp; F, cornified cell, from rootsheath; G, horny diaphragms in the quill.

The section of the *shaft* of a fully-formed feather presents exactly these constituents except the cuticle; the centre is occupied by *medullary substance* (*fig.* 317. B, *a*), composed

* See Bröcker (Reichert, Bericht. Müll. Archiv. 1849).

of a coarsely granular horny substance excavated by polygonal cavities of about $\frac{1}{1000}$ inch in diameter, frequently if not invariably containing air, which adds to the dark hue (by transmitted light) arising from the granular opacity of the horny matter. At its edges, this tissue passes into the *cortical substance*, which, in a transverse section (*fig.* 317. D) appears as a clear, homogeneous or slightly granular mass, dotted over by minute apertures, about $\frac{1}{10000}$ in. in diameter, and $\frac{1}{3000}$ in. apart. In a longitudinal section, on the other hand (*fig.* 317. C, *b*), the general mass appears obscurely striated in a longitudinal direction; and in the place of the circular apertures, we see elongated fissures, somewhat narrowed at each extremity, whose transverse sections constituted these apertures. The pointed ends of the fissures were continued by a line which could frequently be traced into some other fissure above or below, so that I conceive the fissures are in reality more or less complete canals.

The *quill* of the feather is entirely composed of cortical substance; the *barbs* have the same structure as the shaft; the *barbules* present both cortical and medullary substances in a rudimentary condition. Each barbule in fact (*fig.* 317. E, *e*) exhibits along its axis a series of oval cavities, the remains of cells like those of the medulla, while its lateral portions are composed of striated horny matter like that of the cortex, and are produced into the curved and hooked lateral *processes* (*f*).

The polygonal cells of the medullary substance are produced from the indifferent tissue of the pulp in exactly the same manner as those of an ordinary horny, cellular ecderon from that of the *rete mucosum*: that is to say, the periplast increases, and becomes marked out into polygonal areæ; it then acquires a horny consistence, and a stronger and stronger definition along the lines of demarcation, until polygonal "cells" (as in *fig.* 317. B, *a*) are formed. The walls of the latter now thicken and become granular; the endoplasts disappear, and at length nothing is left but the honey-combed perfect medullary substance. The mode of formation of the *cortical substance* is the inverse of this. On examining the line of junction (*fig.* 317. B) of the pulp (*c*) with recently formed cortical substance (*b*), it is observable that the endoplasts do not become surrounded by cell cavities, but that the periplast acquires a granular, longitudinally fibrous, appearance; while the endoplasts, though they are occasionally visible in the striated mass, soon completely disappear.* The elongated cavities or tubuli do not at first exist in the cortex, but are the result of a secondary vacuolation, and so far as I have been able to observe, have no relation with the pre-existing endoplasts. In fact, these canals, like those in the hair-shaft, the clefts in the fenestrated rootsheath, and the canaliculi of bone, must be regarded as the results of a secondary vacuolation. The feather sac resembles that of the hair in all essential points of structure, except that the relations of the layers of the inner rootsheath are different. As in the hair, two layers may be distinguished in the inner rootsheath, an outer, strong, dark, horny membrane corresponding with the fenestrated membrane, and an inner delicate flexible layer, corresponding with the inner horny rootsheath. The former has a structure intermediate between that of the two layers of the inner rootsheath in the hair, consisting of irregular polygonal plates, which retain the remains of their endoplasts (*fig.* 317. F), as in the inner layer of the horny rootsheath, and do not become separated by fissures; while they resemble the plates of the outer horny rootsheath in their thickness, complete cornification and striated appearance.

The inner layer of the horny rootsheath is a delicate, often granular membrane, which closely invests the outer surface of the feather, and from presenting a cast of its elevations and depressions, has been called the outer "striated membrane" of the feather sac (*suprà*, § 2.) It is a sheet of horny matter, in which traces of closely-set endoplasts are discoverable. The inner (*fig.* 317. E, *d*) "striated membrane" is a membrane having a similar structure, possessing similar relations to the inner surface of the feather, and which is continuous with the so-called "pith" in the quill of a fully formed feather. The mode of development of these rootsheaths is identical with that of those in the hair, and therefore requires no further elucidation here.

Tegumentary glands. — The other conversionary productions of the ecderon which we have to consider, are the glandular appendages, which are always diverticula of the cellular ecderon inwards.* Under this head I include only those small glandular organs which, so far as we know, have no reference to any other functions than that of cutaneous transpiration or fatty secretion, referring to the articles on special divisions of the animal kingdom for an account of those organs, such as the "water vessels" of Echinoderms and Trematoda, the nidamental glands of Mollusks, the genital glands of Vertebrata and Insecta, which might strictly be regarded as productions of the integument.

Tegumentary glands in this limited sense are somewhat rare among the Invertebrata. They have, however, been observed in the Annelids, where they consist of delicate tubes, terminating internally by a blind extremity containing a single nucleated cell. Such glands exist on the ventral surface of the head and foot discs in Piscicola, and are scattered all over the body in Clepsine and Nephelis. Similar glands are found opening upon the ventral surface of Argulus foliaceus.

* Compare Schwann, Untersuchungen, &c.

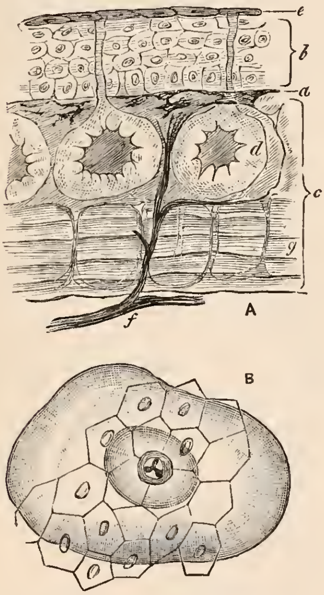
* Unless, indeed, these simple "mucous cells," described by Clark and Leydig in Fishes, and which are merely modified cells of the cellular ecderon, should be regarded as glands.

Simple cœcal glands are scattered over the whole surface of the body of the Procession Caterpillars, opening at the points of the hairs; on the sides of the body in Myriapods, on the joints of the legs in Beetles and Bugs.

In Mollusca a peculiar, probably glandular, canal exists in the foot of certain Lamellibranchs, and glandular cœca have been observed in the lower surface of the foot in Paludina. A ciliated canal runs in the foot of Pulmonata, and receives glands on each side. The existence of cutaneous glands in the Cephalopods appears doubtful—at least, H. Müller could only find them as shell glands in the expanded arms of Argonauta.

Among the Vertebrata, Fishes, Ophidia, Chelonia and Birds, appear to possess no proper cutaneous glands*; in Sauria they attain a very slight and local, but in Batrachia and Mammalia, an immense development. In the frog, the whole surface

Fig. 318.



The cutaneous glands of the Frog. A, section; B, superficial view.

of the ecderon is beset with minute trifid apertures, so disposed between three epidermic cells, as to present a singular resemblance to the stomata of plants (*fig.* 318. B). These lead directly into spherical sacs (*fig.* 318. A. *d.*), which are lined by a continuation of the cellular ecderon, and lie in the superficial part of the enderon above its stratified layer (*fig.* 318. A. *g.*) (*vide infra*). Nerves (*f*) and vessels penetrate the latter to reach the superficial layer of the enderon, and ramify among these close-set glandular sacs. The sacs usually contain only a clear fluid*; they are contractile, and may be made to expel their contents by irritation of the nerves distributed to them.†

In Mammals, we meet with two kinds of cutaneous glands, sebaceous and sudoriparous. The former are almost invariably developed in connection with the hair sacs, consisting in fact of diverticula of the Malpighian layer of the cellular ecderon of the upper portion of these sacs, whence their position is always superficial. The innermost cells of the solid process become filled with fat—break down, and pour their contents into the hair sac itself, by whose aperture they make their exit. Sometimes, as in the hairs of the head in man and in the pig's bristles, the sebaceous glands are very small and simple, while in other localities they throw out processes, and assume the appearance of complex racemose glands, disposed like rosettes around the hair-sac, from which they are developed.

Sudoriparous glands.—These glands, like those just described, are, as Gurlt pointed out, simple, elongated processes of the deep layer of the ecderon, differing from the sebaceous glands chiefly in producing a clear fluid, instead of a fatty secretion. As Kölliker has shown, however, no line of demarcation is to be drawn on this ground, the secretion of the axillary sudoriparous glands in man being an essentially sebaceous substance. The sudoriparous glands are cylindrical cœcal tubes varying, in man, from $\frac{1}{100}$ to $\frac{1}{500}$ of an inch in diameter, whose walls are either thick or thin. In the former case they consist of a simple ecderonic cellular coat, contained within a prolonged sheath, formed by the uppermost layer of the enderon, and, like it, composed of a homogeneous or indistinctly fibrillated periplast, with imbedded endoplasts. Outside this, or rather forming part of it, is a layer of longitudinally-disposed smooth muscles, and the whole is coated, like the deep surface of the rest of the enderon, by a more or less distinct layer of connective tissue. In the thin-coated glands the muscular layer is absent, but the cellular ecderonic coat is frequently so thick that they possess no cavity at all. The thick-walled glands are met with in man in the axilla, scrotum, anal region, &c.; while those of the rest of the body are almost entirely of the thin-walled description. The glands terminate superiorly in undulating canals, which reach the surface of the enderon, and are continued to that of the ecderon by oblique channels excavated in its substance between its cells. Inferiorly, they form close coils, which lie in the subcutaneous

* Dr. Clark, in his excellent account of the skin of the eel (Trans. Mic. Soc. 1849), describes cutaneous glands in that animal. The so-called "glands" of the lateral line, however, have since been shown by Leydig to have a very different structure; and I confess I have not been able to convince myself of the existence of the other glands described by Dr. Clark. I can find nothing like them, except the strong perpendicular semi-elastic bands, which traverse and unite the bundles of connective tissue in this as in other fishes.

* Stated by Bergmann and Leuckart to have an irritating property in Triton.

† Ascherson: Haut-drüsen d. Frösche, Müller's Archiv, 1841. Czermak: Haut-nerven d. Frösche. Ibid. 1849.

areolar tissue, and receive twigs from the vessels in their neighbourhood.

In the other Mammalia, the general structure of the sudoriparous glands is as in man. In the sheep, according to Gurlt, they present the same coiled arrangement, while in the ox and dog they are straight and simple. In the ox they have rounded, dilated extremities, and are everywhere similar in shape and size. On the hairy parts of the body of the dog, they are small simple cœca, which are very difficult to discover; while on the ball of the foot of this animal they are very large and resemble those of man. Very large sudoriparous glands have likewise been observed upon the horse's prepuce.

Scales of fishes. — In the Ganoid fishes *Accipenser* and *Polypterus* the substance of the scales is composed of ordinary bone whose superficial layer is only denser than the rest, and exhibits a local developement of fine branching tubuli; but in other fishes, two, if not three, distinct layers are usually distinguishable in the scales.

In many Plagiostomes, for instance, the placoid scales have the same composition as the teeth, consisting of a superficial layer of nearly structureless dense "enamel," or as Prof. Williamson more conveniently terms it, "Ganoin," while the deeper substance is composed of a tissue in every respect similar to dentine, whose innermost portion in some cases passes into true bone, — an addition which might be compared to that of the cement in the teeth. Leydig, indeed, has shown that the resemblances between the scales and the teeth of Placoid fish extend even to their mode of developement. If the pulp contained in the central cavity of the spine-like scale of a *Raia clavata* be pulled out, globular calcareous masses of $\frac{1}{1000}$ of an inch and upwards in diameter, and either solitary or adhering together in masses, will be found to be attached to its surface. "These globules are exactly analogous to the dentine globules described by Czermak, which in human teeth afford the formative material for the matrix of the dentine. What, however, appeared to me especially worthy of notice was the circumstance, that the most distinct and beautifully branched canals, having exactly the same appearance as those in the substance of the spine, were already visible in these isolated calcareous bodies, and on carefully examining the fine processes of the canals, no doubt could exist that they were only interspaces or gaps. On carefully adjusting the focus, in fact, it was obvious that one of these large calcareous globules is itself only an agglomeration of many smaller globules, and it could be observed that the gaps left between the latter became the fine processes of the tubules. From these facts, I believe that the correct mode of conceiving the growth of the substance of the spine is, to suppose that the calcareous matter is excreted from the vessels of the pulp, and then in all probability combined with organic matter, runs into smaller masses; these unite together into larger ones, and become applied to the inner surface of the central cavity, coalescing, and thus adding to the thickness of the spine. Between the calcareous globules, however, canalicular gaps or tubules remain, which form a connected network and communicate with those branched cavities which already exist in the spine.

The scales of the Sharks and the dermal spines of the Rays, then, (and I would draw particular attention to this result,) are perfectly identical in structure with the teeth, even to the absence of nerves in the pulp, and must be united in the same structural group. I have already (On the Skin of Freshwater Fishes, Zeitschrift für Wiss. Zool. B. iii. H. 4.) pointed out the close affinity between the scales of a number of osseous fishes and their teeth: and scales likewise present globules of calcareous matter, which become fused together to form the homogeneous substance of the scale. A process, corresponding with that which occurs at the surface of the pulp in the teeth and cutaneous spines, here takes place from the surface of the sac of the scale (Schuppentasche). The scales of osseous fishes, the spines of the Rays, and the scales of the Sharks, therefore, all belong to the series of dental structures, which in no respect interferes with the entrance of true bony tissue (like the "cement" in the higher animals) into their composition, as we find to be the case in the scales of the Ganoids (Müller), and in the truly bony semicanals which are attached to the scales of the lateral lines of many fishes." *

For the details of the various modes in which Ganoin, true osseous tissue, and those varieties of tubular, more or less dentine-like tissues, to which Prof. Williamson has given the names of "Lepidine and Kosmine," are combined together in the scales of Ganoid and Placoid fish, I must refer to that gentleman's memoirs, already so often cited.

In the Ctenoid and Cycloid fishes there is a superficial "Ganoin" layer, composed of numerous thin structureless calcified laminæ, which are frequently thrown into folds, papillæ or spines. The deeper substance of the scale is composed of a series of layers of a membranous substance, each layer being composed of parallel fibres which take a different direction from those of the superficial and subsequent layers, so that the fibres of alternate layers cross diagonally. No endoplasts or cells are ever distinguishable among the fibres. In the deepest part of the scale these layers are entirely membranous; but in passing towards the surface, minute lenticular masses of calcareous matter make their appearance in the membranous substance. As Prof. Williamson justly states, these lenticular bodies are not developed between the membranous fibres and lamellæ, but in them: "they commence as a small calcareous atom, and in-

* Leydig: Rochen und Haie, 1852.

crease in size by the external addition of new concentric laminæ; the direction of the latter not being parallel with, or having any reference to, that of the laminæ of fibrous membrane with which they so amalgamate; thus they are not depositions from, but growths in the membrane; which growths, as they increase in size, retain their primitive tendency to assume a lenticular form." Following the layers of the scale outwards, these isolated calcareous deposits not only enlarge, but ultimately become fused together, forming at length either a continuous calcareous mass in each layer, or presenting fissures which in some cases traverse the original lenticular calcareous deposits, in others are interstitial to them. I think one cannot but be struck with the complete analogy between the structure and mode of developement here described and those which I have previously shown to obtain in the calcified tegumentary organs of the Mollusca and Crustacea. The ganoin layer corresponds very closely with the "epidermis" of the shell or test; the middle laminated calcified substance is formed by the fusion of concentrically laminated concretions deposited in a membranous matrix in the Fish, the Mollusk, and the Crustacean alike; while the deep uncalcified layers of the scale are represented by the "horny" laminæ which have escaped calcification in Haliotis or Unio, and still more closely by the fibrillated uncalcified layers of the Crustacean test.

Structure of the enderon. — The enderon of the Invertebrata is usually entirely composed of rudimentary connective tissue or of mere indifferent tissue, consisting, in the latter case, simply of a matrix with imbedded endoplasts, while in the former it is produced into plates and bands, never exhibiting, however, the peculiar bundles and elastic fibres which are met with in fully formed connective tissue.

In Paludina, according to Leydig, the pigment masses, which lie on the surface of the ecderon, are connected by "clear large cells, with a small parietal nucleus." From their occurrence, wherever in the higher animals connective tissue is found, Leydig calls them "Binde-substanz-zellen"—"Connective tissue cells;" but, as he himself points out, they frequently contain carbonate of lime, and their relation is rather, like that of the similar cells in Piscicola, to fat.

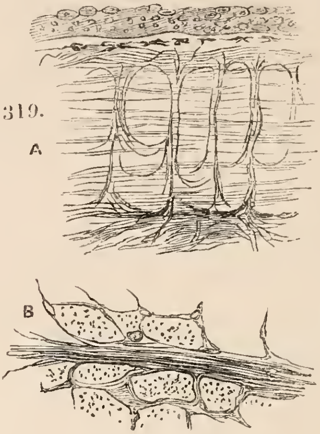
A wonderful complication of structure is attained by the skin of the Cephalopoda. According to H. Müller *, who has recently made some careful investigations on this subject, there lie beneath the cellular ecderon in these animals: 1st, a fibrous layer, usually colourless, but occasionally white and glittering. 2nd, the layer with the chromatophora (*vide inf.*). 3rd, beneath these a peculiar layer, which gives rise to the colours produced by interference, the metallic lustre, and intense whiteness of many localities. It consists frequently of regular plates, which evidently proceed from nucleated cells. 4th, deeper still lie the larger bundles of connective tissue, the muscles and the vessels.

In the Vertebrata, the superficial layer of the enderon is similarly composed of indifferent tissue, and of rudimentary connective tissue; the former passing gradually into the latter, as

Fig. 319.

A

B



Enderon of the Skate.

we trace it inwards, developing its elastic element to a greater or less extent, and acquiring a more or less distinctly fascicular arrangement of its collagenous element. In the higher Vertebrata, these bundles are usually disposed as an irregularly felted mass; but in Fishes and Batrachia, they form regularly superimposed horizontal strata, tied together by perpendicular columns, which penetrate the interspaces of the bundles, and spread out into the irregular connective tissue on the deep and superficial surfaces of the stratified mass (*fig.* 319. A). On the addition of acetic acid, it is seen that the boundaries of the strata are formed by irregular bands of elastic tissue, in which the remains of the primitive endoplasts may be seen (as in fibro-cartilage), whose strongest fibres are horizontal, though they send out others irregularly in all directions. The perpendicular columns are likewise composed of bundles of pale elastic fibres (*fig.* 319. B), and if the intersection of the horizontal with the vertical divisions be carefully examined, it is seen that the former are, as it were, given off by the latter, which thus gradually break up and thin out, terminating above and below in the elastic fibres of the unstratified superficial and deep layers. A horizontal section of this portion of the enderon presents a very peculiar appearance, the transparent vertical columns looking like radiating spaces, as which they were, in fact, at first described.

Pigment of the enderon. — The enderon presents scattered masses of pigment, sometimes contained in cells and sometimes free, in many Invertebrata (Annelids, Trematoda, Echinoderms, Crustacea, Mollusca). In other Invertebrata and in the higher Vertebrata, the pigment is confined to the ecderon. In Fishes and Reptiles, however, a well-marked layer of pigment lies at the surface of the enderon in the form of scattered granules

* Bericht, &c. Zeitschrift für Wiss. Zoologie. 1853.

and of irregular more or less stellate masses which are not enclosed in cells. The silvery lustre of the skin of fishes is due to minute rods which constitute a layer at this surface, and should probably be regarded as a peculiar form of pigment granules.

In the Cephalopoda and some Gasteropoda among the Invertebrata, the integument undergoes during life the most extraordinary variations of colour, becoming overspread with successive clouds of the most vivid hues. These are produced by the contraction and expansion of peculiar sacs — the *chromatophora*—containing masses of pigment granules. According to H. Müller, (whose observations I have recently had the opportunity of repeating,) these are sacs attached to whose walls are contractile fibre cells arranged radially, and frequently anastomosing with those of other cells. They do not always contain pigment, but frequently present a distinct nucleus. Several layers of these chromatophora of different colours are frequently disposed, one over the other, in a given portion of the skin, and produce by their different states of contraction, relatively to one another, successive changes in the colour of the spot.

Among the Vertebrata the Chamæleon, as is well known, presents similar phenomena.

Papillæ of the enderon. — The enderon is frequently produced into conical or cylindrical processes, which either merely contain a vascular loop, or are supplied, in addition, with special nerves. In the Invertebrata, we find, in the processes of the mantle into the shell of the Brachiopoda described by Dr. Carpenter, organs which, I have no doubt, must be regarded, like the corresponding processes in the Ascidians, as vascular papillæ. Among the Articulata like processes extend, in the Crustacea, through the whole thickness of the integument to its surface, giving rise to the colourless spots observable on the shell of the crab, for instance. I imagine, however, that these spots were usually occupied by a hair when the shell was thin. In the Mollusca, the marginal processes of the mantle of the Lamellibranchs and Gasteropods, the papillæ of Onchidium, &c. and those of Tremoctopus (H. Müller) are very probably both vascular and nervous papillæ like those of fishes.

Among the Vertebrata, fishes present large projecting papillæ, particularly about the region of the lips and operculum, which are both vascular and nervous. Simple papillæ (nervous?) are scattered over the surface of the body in Plagiostomes and some Ganoid fishes.

I am not aware that papillæ have hitherto been observed on the integument of Birds and Reptiles. In most Mammals, they are very small, if they exist at all, upon the general surface of the body, attaining a considerable size only in such organs as the ball of the foot (Cat, Dog), or on the muzzle. The Cetacea, however, appear to make a remarkable exception to this rule; it is stated (Heusinger, Breschet, and Roussel de Vauzème) that the very thick integument of these animals is traversed by vascular and nervous papillæ, four or five lines long, which extend as far as the outer horizontal horny layer of the ecderon, so that a horizontal section of the ecderon is like that of a horse's hoof. In man, again, the papillæ are, as is well known, so abundant as to have given rise to the term *pars papillaris*, for the superficial layer of the ecderon. The structure of those which appear to possess special nervous functions will be considered below.

Sensory appendages of the enderon. — Very little is known of the ultimate distribution of the nerves to the integument in the Invertebrata, but we are indebted to Leydig for showing that in certain Crustacea, Insecta, and Mollusca, it is very similar to what occurs in the vertebrate classes. Thus in *Argulus foliaceus* the peripheral nerves become pale, and divide, and at the point of division there is a 'nucleus' as in the embryonic fibres of the frog. In *Artemia salina*, *Branchipus stagnalis*, and in the Heteropod Mollusk *Carinaria*, the termination of the tegumentary nerves is essentially similar. The larva of the Dipterous insect *Corethra*, presents even peculiar sensory appendages, in the delicate plumed hairs which beset the sides of the body. These are articulated in the ordinary way, and have an internal ligament, a sort of spring, attached to their base, which is enlarged and receives the enlarged and cellæform termination of a nervous twig. It will be obvious that this arrangement is peculiarly fitted for communicating the slightest vibration to the nerves.

In the Vertebrata (fishes, reptiles, man), the ordinary mode of termination of the integumentary nerves is in one or two plexuses, whence the fine terminal branches proceed, and end by dividing into minute branches indistinguishable from the imperfect elastic fibrils of the enderonic tissue. Loops have also been observed, but it is impossible to say whether, in any case, these are real terminations or not. Gerber and Kölliker have also described "nerve coils" in animals, and in the conjunctiva and lips of man.

The simplest form of sensory appendage in the Vertebrata is presented by the large papillæ of fishes, into which a bundle of nerve fibres enters, some of which terminate in the papillæ, while others, whose looped bands may be readily distinguished, probably pass out again.

In certain fresh-water fishes (Barbus, Leuciscus), Leydig has described papillæ of this kind, which have a cup-shaped depression at their extremities, lodging a globular mass of what he describes as modified epithelium.

Special modifications of the tissue of the papillæ for sensory purposes in the fingers, tongue, lips, &c. of man have lately been discovered by Meissner and Wagner, and described by them, under the denomination of the *Corpuscula tactûs*. Kölliker, who doubts their special relation to the tactile function, on the other hand, prefers to call these bodies, *axile corpuscles*. They are simply ovoid masses of imperfect connective tissue occupying the centre of the papillæ, and further distinguished by having their endoplasts and imperfect elastic

Fig. 320.

A papilla with its Corpusculum tactûs surrounded by three vascular papillæ.

fibrils arranged transversely to the axis of the papilla, so that they appear to be made up of transverse superimposed laminæ (*fig.* 320.). One or two dark-contoured nerve tubules come up through the base of the papilla, and running along one side of the corpuscles, thin out and terminate, without, so far as I have been able to see, entering its substance. In fact, these nerve tubules are, as Kölliker pointed out, accompanied by a delicate neurilemma, and the axile corpuscle itself appears to me to be nothing more than the enlarged end of this neurilemma.

In Birds, a large proportion of the tegumentary nerves terminate in bodies which are, on the one hand, related to these axile corpuscles, and on the other to the well-known Pacinian bodies (*fig.* 322). They are, in fact, usually described under the latter name; but their small size and superficial position, the paucity of their concentric lamellæ, and the transverse striation of the solid central axis, ally them closely with the corpuscula tactus. They are found in the skin around the sacs of the feathers, in the beak, and in the interosseus spaces of the fore-arm and leg.

A special article (Pacinian Bodies) has already been devoted to the organs of this kind which are met with in Mammalia, and it need only be added here, that late researches have shown that the Pacinian bodies of mammals, like those of birds, are solid masses of rudimentary connective tissue; the appearance of capsules and of a central cavity, arising merely from the arrangement of the elastic element and the extreme transparency of the collagenous substance.* They are in fact nothing but thickened portions of the neurilemma, and the nerve which they enclose either passes through them, or more usually terminates, more or less abruptly, in the central solid axis.

In the article on the Pacinian Bodies reference is made to the peculiar organs described by Savi in the Torpedines. These Savian bodies, in fact, are little more than Pacinian bodies converted into sacs by the development of a cavity between their central and peripheral portions. Now Leydig has discovered that these Savian bodies do not stand alone, but that they form a part of a great series of peculiar integumentary sensory organs, which are most characteristically, if not solely, developed in the class of Fishes — the so-called *mucous canals* and *follicles*. It has long been noticed, in fact, that in osseous fishes one series of the scales along the sides of the body differ in their structure from the rest, giving rise to what is called the *lateral line;* and that a canal runs beneath these scales from the tail to the head on each side; that then becoming connected with its fellow by a transverse branch over the occiput, each canal passes forward on the sides of the head, dividing into two principal branches, one of which following the course of the suborbital bones terminates at the end of the snout, while the other passes down on to the lower jaw. Similar organs, but having a more complicated arrangement, are known to exist in the cartilaginous fishes; but it is commonly supposed that these canals and follicles secrete the mucus with which the skins of fishes are lubricated. However, in a very beautiful series of researches, Leydig has shown that the mucus is furnished by the cellular ecderon, and that the so-called mucous canals and follicles are sensory organs. The limits of this article will not permit me to enter into any of the details of structure of these organs, but they may all be described generally as sacs or canals lined by a cellular investment, like that of the skin upon which they open, and filled with a more or less gelatinous substance. If the organ be a sac, a single protuberant knob, if a canal, a series of them project into the cavity. Each knob is covered by a coat consisting of tiers of much-elongated cylindrical cells. Its substance consists of more or less gelatinous connective tissue, and it receives a nerve (a branch of the fifth or of the vagus), whose fibres divide and become lost in its tissue. In the osseous fishes this nerve usually perforates the peculiarly modified scale of the lateral line, which supports and encloses the canal at these points. In the cartilaginous fishes, the canals have sometimes special fibro-cartilaginous coats; or if sacculi, a number of them may be contained in a common cartilaginous investment, as in the Chimæra. Leydig insists with great justice on the identity of the structure of these organs with that of the semicircular canals of the ear.

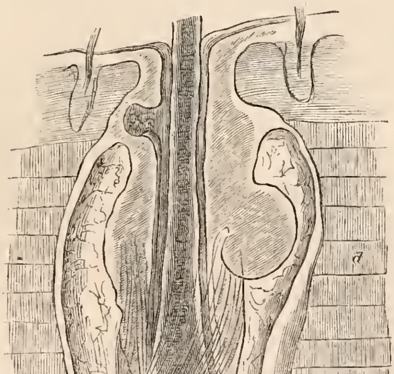
The connection of these sacs and canals with the corpuscula tactus and Pacinian bodies

* This fact was ascertained and stated independently and contemporaneously in 1853, by Leydig and myself. See Quarterly Journal of Micr. Science, No. V., and Siebold and Kölliker's Zeitschrift, B. v. Heft 1.

appears to me to be clear; for the knob which projects into the cavity of the mucous canal is homologous with the central "nucleus" of the Savian body, and this with the solid axis of the Pacinian body, and with the corpusculum tactûs, so that the "tactile" sac of the Chimæra, *e. g.*, may be said to be a tactile corpuscle which is connected with the surface of the integument.

No organ at all resembling these has certainly been met with, above the class of Fishes, in either Reptilia or Birds, but in Mammalia there are structures which must, I think, be placed in the same category. About the lips and nose of almost all mammals in fact, there are certain long, strong hairs, the vibrissæ or "whiskers" (*fig.* 321.). These in their general structure resemble ordinary hairs, but the sac of each, instead of lying free in the enderon, is enclosed in a second thick sac, composed of firm, dense, connective tissue, which attains at times an almost cartilaginous hardness. A looser areolated tissue connects this with the outer surface of the proper hair sac, and supports an abundant vascular network proceeding from vessels which enter at the deep end of the sac. Furthermore, a very considerable nerve pierces one side of the "sclerotic" coat near this end, and passes to the surface of the proper hair sac, upon which it spreads out and forms a nervous expansion, its fibrils dividing and subdividing, and so terminating.

Fig. 321.



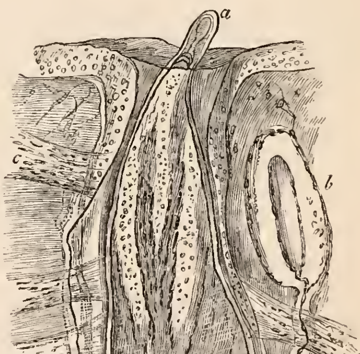
Vibrissa from the snout of the Mouse.
a, "sclerotic" sac; *b*, hair-sac; *c*, nerve-trunk; *d*, muscular fibres.

Considering the different habits of life of the mammal and the fish, I think one cannot but be struck with the similarity of plan between their vibrissæ and the "tactile" canals. The sensory impression is conveyed to the gelatinous contents of the canals in the fish by the vibration of the dense medium in which it lives; while in the mammal the impulse is communicated by the contact of some external object with a long elastic hair lever; but the final arrangement for the receipt and appreciation of the impressions is essentially the same in each case, nor indeed does it differ from that which is met with in the highest organs of sense.

Muscles of the enderon.—In the Invertebrata the great majority of the muscles are, as is well known, inserted into the integument, but those which are attached to the chromatophora of mollusks and to the spines of annelids and other worms, might be regarded as belonging more especially to the integumentary system.

In Fishes and Reptiles the superficial layer of striped muscles of the body is always more or less connected with the integument; but hitherto no unstriped fibres appear to have been detected in it. In Birds, however, the unstriped muscles attain a very great development, forming a thick layer whose bundles (*c*) run between and are attached to the sacs of the feathers (*fig.* 322.).

Fig. 322.



Pacinian body (*b*) and feather-sac (*a*) from the base of the mandible of a pigeon. *c*, muscles of the feather sacs.

In the majority of Mammals there is a special tegumentary striped muscle, which attains an enormous development in the hedgehog, while a mere rudiment of it remains in man, as the platysma myöides. Here, however, the striped "*peaucier*" muscle is replaced by the unstriped bundles which, as Kölliker has shown, run from the upper layer of the enderon to the bases of the hair sacs, and effect the various movements of which the hairs are capable.

Calcareous deposits in the enderon.—Deposits of this kind are very frequent in the Invertebrata. In the Pulmonate and some Gasteropod Mollusks, for instance, globular masses of carbonate of lime are scattered through the enderon, and would almost seem to take the place of fat. In nudibranchiate mollusks, such as the Doridæ, spicula of like nature are met with, and these sometimes unite into true internal shells, as in the genus Villiersia. The greater part of the skeleton of the Actinoid polypes, and the whole of that of the Echinoderms, is composed of calcareous networks of this kind, and globular masses of calcareous matter are scattered through the enderon of the Tæniadæ, though the clear spherical bodies observed in these worms are by no means always of this nature. Whether these enderonic calcareous deposits ever take place in the Vertebrata appears to me to be, as I have said above, an open question, only to be decided by a very careful examination of the mode of growth of their so-called "dermal" bones.

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(*T. H. Huxley.*)

RUMINANTIA (Lat. *ruminare*, to chew the cud), Eng. *Ruminants*; Fr. *Ruminans*; Ger. *Wiederkäuende Thiere*, — a well defined order of mammalian quadrupeds, presenting the following essential characters: Upper jaw in nearly all cases destitute of incisor teeth, their place being supplied by a callous pad, while the lower jaw has six incisives; canines inconstant; molars usually six on each side of both jaws, with flattened crowns surmounted by two double and irregularly crescentic folds of enamel. Stomach compound and divided into four cavities, so as to provide for the ruminating act. Cœcum large. Placenta generally in the form of cotyledons. Feet ungulate and bisulcate.

This order forms two natural divisions, comprising the Hornless ruminants (akeratophora, Col. H. Smith) which are few in number, and the Horned ruminants (keratophora) which are very numerous. The English naturalist Ray, who was the first to propose a classification based on philosophical principle, enumerated only fifteen species. Pallas subsequently divided the entire family into six genera, and the Baron Cuvier into eight or nine; but the number of subdivisions held to constitute *genera* by later authorities has been very greatly extended. To serve our present purpose we shall retain only the Linnean and two other genera, which may be conveniently arranged under the five following heads or sub-orders: —

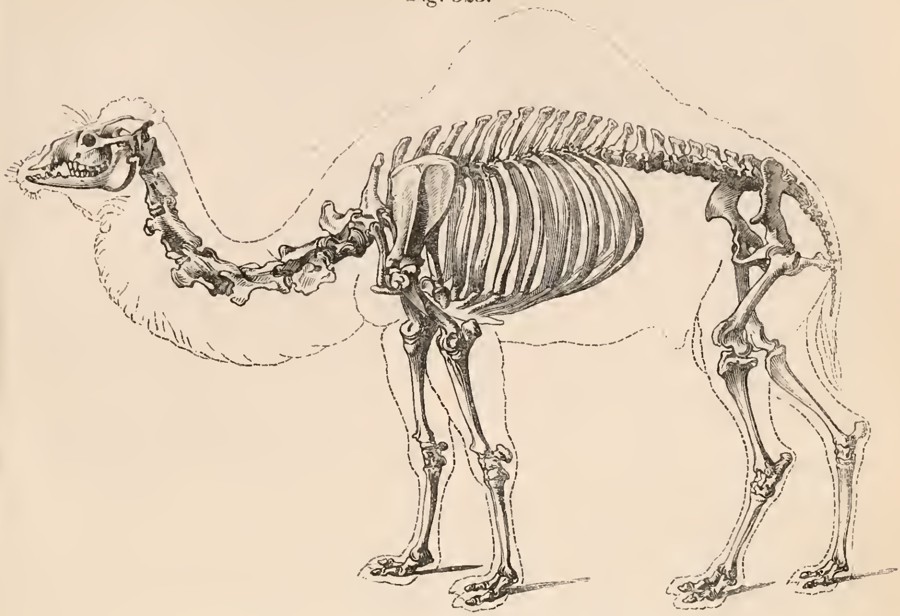
I. Camelidæ -	Camelus -	*Linn.*
	Auchenia -	*Illiger.*
II. Cervidæ -	Moschus -	*Linn.*
	Cervus -	*Linn.*
	Camelopardalis -	*Linn.*
III. Antilopidæ -	Antilope -	*Linn.*
	Catoblepas -	*Smith.*
IV. Œgosceridæ -	Capra -	*Linn.*
	Ovis -	*Linn.*
V. Bovidæ -	Bovis -	*Linn.*

The Camelidæ differ in many important particulars from the horned ruminants, and exhibit an approximation to the Pachydermata. The dental formula is peculiar; thus in the genus Camelus there are,—

$$i.\ \frac{1-1}{3-3};\quad c.\ \frac{1-1}{1-1};\quad p.m.\ \frac{2-2}{1-1};\quad m.\ \frac{3-3}{3-3} = 30$$

and in this respect the Auchenias, or Llamas, disagree only in the number of molars, which is usually fourteen. The distinguishing features of this family depend principally upon the beautiful provision of water-cells in the walls of the paunch or first cavity of the stomach, the absence of horns and the sub-bisulcate feet, which are "callous beneath, and

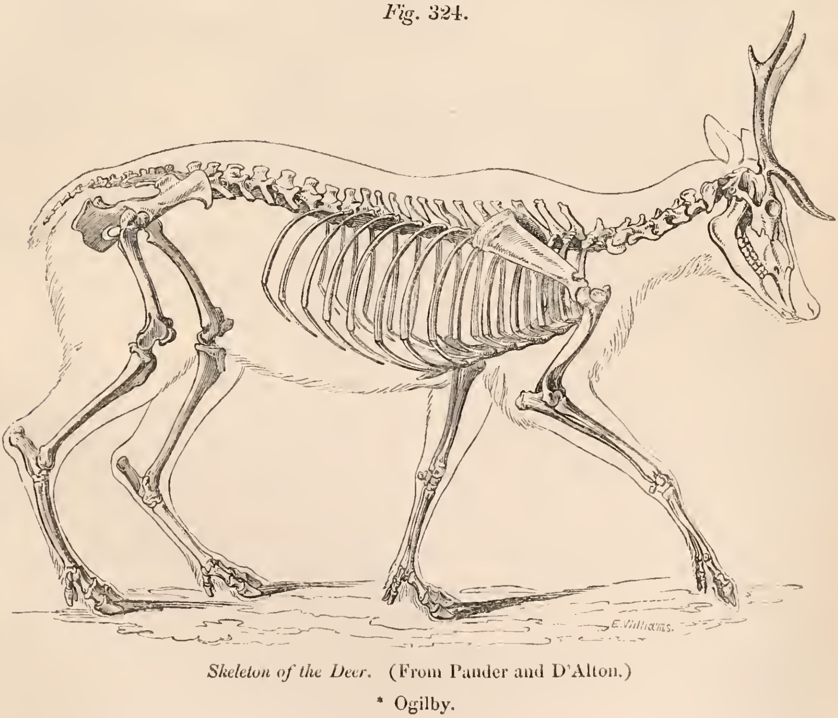
Fig. 323.



Skeleton of the Camel. (From Pander and D'Alton.)

have the toes distinct at the tip from the sole."* The uterine and fœtal membranes are unprovided with the ordinary ruminant or cotyledonoid form of placenta. Professor Owen has demonstrated another remarkable character arising out of the non-development

Fig. 324.



Skeleton of the Deer. (From Pander and D'Alton.)

* Ogilby.

of foramina for the passage of the vertebral arteries through the transverse processes of the lower six cervical vertebræ. This anatomical arrangement occurs in no other existing tribe of mammifers, but in an aberrant form of fossil pachyderm (*Macrauchenia*), Dr. Owen has detected the same anomaly, and has thus established an additional connecting link between the Pachydermata and Ruminantia.

In the classification of the Cervidæ given above we have included two genera not usually considered as forming a part of this family. One of the principal characters of the Cervidæ proper consists in the presence of deciduous horns or antlers: the genus Moschus, however, like the Camelidæ, is hornless; and the genus Camelopardalis is provided with persistent horns which are at all times clothed with a hairy integument. The dental formula of the Cervidæ and all other horned ruminants is usually as follows, —

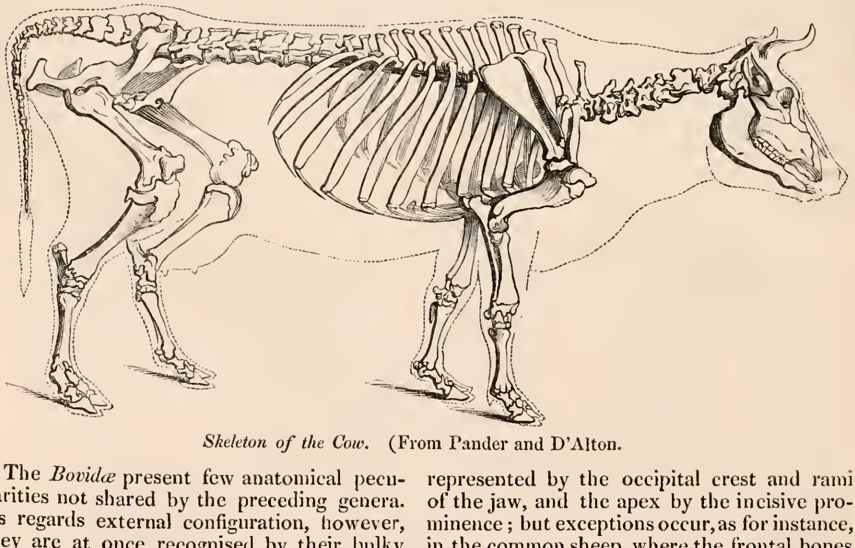
$$i. \frac{0\ \ 0}{3\ \ 3};\ c. \frac{0\ \ 0}{1\ \ 1};\ p.m. \frac{3\ \ 3}{3\ \ 3};\ m. \frac{3\ \ 3}{3\ \ 3} = 32.$$

The Musk-deer tribe have in addition two long and conspicuous canines in the upper jaw, projecting in the males below the mouth. (*fig.* 330.). The male Kijang or Muntjak (*Cervus muntjac*, Zimmerman) has likewise two prominent canines in the upper jaw (*a, fig.* 331.). In the Giraffe there is a complicated glandular and pouch-like structure in the neighbourhood of the ileo-colic valve.*

The Antelopidæ include the greater number of the Cavicornua or hollow-horned division of ruminants in which the bony axis of the horn is solid, persistent, and destitute of cavities or pores. They have, for the most part, a slender figure adapted for rapid progression, and, like the Stags, are further distinguished by the possession of infraorbital glandular sinuses.

Under the term Œgosceridæ (*Œgosceros*, Pallas) we have brought together the closely allied genera *Capra and Ovis.* The Goats are characterised chiefly by their long horns, which are directed upward and backward, are more or less angular in front, rounded behind, and generally marked by transverse bars or ridges. The chin is clothed with a long beard. The Sheep which have no beard differ mainly in having the horns directed at first backward, and subsequently bent spirally forward. Between the toes at the anterior aspect of the feet is situated a special glandular sebaceous sac; this structure is also found in other ruminants, — the Rein-deer, for instance. Neither the Sheep nor Goats exhibit the lachrymal sinuses so characteristic of the majority of the Antelopes and Stags.

Fig. 325.



Skeleton of the Cow. (From Pander and D'Alton.

The *Bovidæ* present few anatomical peculiarities not shared by the preceding genera. As regards external configuration, however, they are at once recognised by their bulky massive size, the broad muzzle, and powerful limbs (*fig.* 325.). The horns are directed laterally, with an inclination upward more or less curved. In their habits and in the structure of the skin, some of the species, the Buffaloes, for example, approach the pachydermatous type.

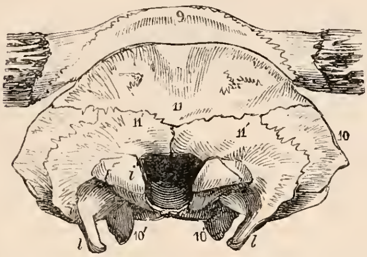
Osteology. — The general form of the skull in ruminants, when viewed laterally, is that of an isosceles triangle, the base of which is represented by the occipital crest and rami of the jaw, and the apex by the incisive prominence; but exceptions occur, as for instance, in the common sheep, where the frontal bones are so much arched as to produce a somewhat oval figure, and in the camel, where, owing to the abrupt termination of the nasal and sudden depression of the intermaxillary bones, an obliquely quadrilateral form is the result (*fig.* 334). The forehead is usually straight and elevated, the orbits are placed wide apart, and the muzzle, except in Bovidæ,

* See "*Glands of Intestine*" in this Article.

is attenuated and compressed. Throughout the whole order there prevails considerable disparity as respects the cranium and face; the bones of the latter occupy fully two-thirds of the entire length of the skull, and the area of the face on section is nearly double that of the cranium.

Bones of the cranium. — Eight bones enter into the composition of the adult cranium; viz, an occipital, a parietal, two frontal, a sphenoidal, an ethmoidal, and two temporal; and, in addition to these, some species are provided with two ossa triquetra or interparietals.

Fig. 326

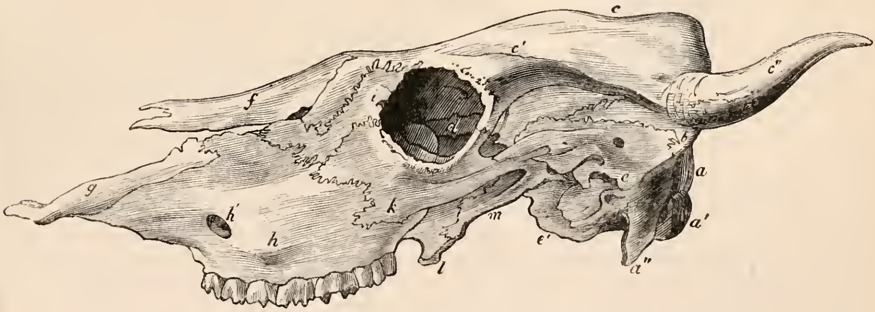


Skull of the Ox viewed from behind. (From a specimen in Lond. Coll. Surg. Museum.)

The *occipital* bone (11, *fig.* 326.), as in most of the mammalia, is originally divided into four, one superior, one inferior, and two lateral pieces (11′, *fig.* 326.). These become early consolidated, and in the calf at the time of birth they are firmly united together and to the parietal and interparietal bones lying immediately in front. The occipital crest is prominent in the Llamas, and still more fully developed in the true Camels. In Bovidæ the crest corresponding to the occipital is formed by the junction of the parietal and frontal bones, the superior occipital remaining flat. In ruminants generally, the paramastoid processes (*l fig.* 326.) are much elongated, falciform, and curved inwards, and between these and the occipital condyles (*i*) a very deep fossa intervenes. In Camelidæ, at the angle formed by the union of the petrous portion of the temporal with the lateral and superior occipitals there is a large opening on either side. In this family the anterior condyloid foramina are of moderate capacity, but in Cervidæ they are of great size and sometimes four in number, in which case two remain small. In Œgosceridæ and Bovidæ they are also large and occasionally double.

The *parietal* (9*) is single, and with a few trifling variations, is articulated to the cranial bones in the usual manner. The lambdoidal or parieto-occipital suture lies considerably in front of the crest, except in Bovidæ, where it lies below, and is separated from the frontal suture by the intercalated and narrow wedge-shaped parietal bone. The Œgosceridæ have the parietal in the form of a flattened band, encircling the cranium and extending between the orbitar wings of the sphenoid on either side (*b*, *fig.* 335.). It is broader in the goats than in the sheep. In Bovidæ the parietal does not extend so far forward (*b. fig.* 327.). In the Giraffe the lateral processes of the parietal are narrowed

Fig. 327.



Skull of the Ox, viewed laterally. (From Spix.)

to a mere point, but the body of the bone which reaches from between the horns as far back as the occipital crest has a longitudinal diameter of fully six inches. The coronal or fronto-parietal suture in this species and a few other genera is situated in a line with the osseous protuberances which support the horns. It is most frequently placed behind; in the Gazelles, however, it appears in front.

The *frontal* bones (8) are of large size and great breadth; this latter feature being more especially manifest in the Camels, the Sheep, and certain bovine species. In the Camelidæ they extend backward between the anterior divisions of the parietal bone, and in front they are articulated to the lachrymals by a transverse suture, which is less extended in the Llamas than in the true Camels. In the Llamas and in the genus Moschus a small part of the frontal is connected to the superior maxillary. There are several supra-orbital or frontal foramina (*c*) with rounded orifices, which in the Camels are placed near the middle line and at the centre of the forehead. In the Llamas these openings are placed rather farther back and united by a longitudinal groove. The frontals are ele-

* The numerals here refer to all the subjoined figures of crania with the exception of *figs.* 327. and 335.

vated posteriorly in Bovidæ (*c*, *fig*. 327.) and prolonged toward the occipital crest, in the formation of which they apparently contribute,—a circumstance giving rise to the peculiar physiognomy characteristic of the group. The osseous protuberances supporting the horns, of which we shall speak more particularly when describing the latter in detail, take their origin in most cases from the frontal bones. In the Giraffe the slight eminences analogous to the osseous cores are partly formed by the parietal bone, the coronal suture passing directly through the centre from side to side (*fig*. 328.) ; the an-

Fig. 328.

Front view of the skull of a Giraffe. (From a specimen in Lond. Coll. Surg. Museum.)

terior or central eminence, situated immediately behind the nasals, and in part formed by them, differs in no respect, save as regards its position, from the other two, the elevation in all instances being produced by the expansion of the cranial sinuses beneath. There is a single large supra-orbital canal, having its superior outlet midway between the upper border of the orbit and the central frontal eminence (*fig*. 328.). In Cervidæ generally, the canal opens at the upper surface by a longitudinal furrow (*fig*. 329.), but this is more particularly marked in Bovidæ (*fig*. 333.). In regard to the cranial sutures in Cervidæ, M. F. Cuvier observes that "all those portions, such as the second half of the frontal, the greater part of the coronal, and the occipital or lambdoidal, which surround the base of the core, exhibit an excessive multiplication of interlineations, because the weight of the horns and the shocks to which the parts are exposed require that the bones should be firmly connected" (*fig*. 329).*

The *sphenoid* (12) articulates, except in Bovidæ, with all the cranial bones ; but its orbitar wing, which is largely developed, is concealed in great measure within the cerebral cavity, and covered by the lateral expansions of the frontal bones. In the Camelidæ the pterygoid processes of the sphenoid are directed vertically downwards and terminate in two laminæ, the external one being longer and larger than the internal : the latter process only makes its appearance very low down, and is so closely applied to the external lamina, as to leave scarcely any trace of a pterygoid fossa ; neither is there any space between it and the wing of the palatine bone. In this family the spheno-orbitar fissures and the spheno-palatine foramina are of great size. The optic canals are only separated from the former by a thin osseous partition, and the openings for the passage of the third branch of the fifth pair of nerves are rounded and placed far back. The Cervidæ have the posterior division of the sphenoid developed into an extremely attenuated and short temporal wing, which, nevertheless, is articulated to the parietal, the lateral processes reaching very far forward. The orbitar wing of the sphenoid in the same family separates into two divisions, one extending upwards and backwards, and also uniting with the parietal, the other being prolonged horizontally forward, between the frontal and palatine bones, and terminating anteriorly at the border of an opening which corresponds to the spheno-palatine foramen. In the Giraffe the temporal wing of the sphenoid is short and connected by a well-marked suture to the T-shaped process of the narrow lateral expansion of the parietal ; it approaches very closely, but is not united to the orbitar plate of the frontal as has been conjectured. In the work last alluded to in the foot-note it is stated that the frontal and sphenoid bones are united at an early period, rendering it difficult to make out their limits. In the cranium of a Giraffe about two years old, and at present in our possession, the sutures involved in the union of the above-mentioned osseous segments, fortunately yet remain distinct, and in this individual the orbitar wings of the sphenoid do not divide into two laminæ, as seen in the Stags, but at the floor of each orbit they form a broad, short, and triangular fan-shaped plate, the centre of which is pierced by the hole for the passage of the optic nerve. The spheno-orbitar apertures are round and of enormous size in the Giraffe : in the Stags the spheno-palatine foramina are also large ; and this is more especially the case in Camelopardalis, where they lie concealed behind the molar prominences. In the genus Moschus the anterior sphenoid is largely developed, and its wings form the greater part of the posterior wall of the orbits. The body of

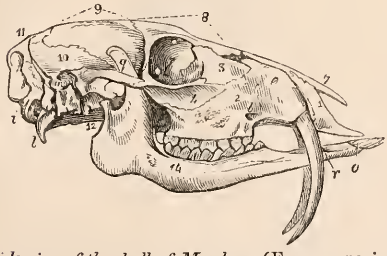
* Cuvier, Leçons d'Anat. Comp., 2de edit. tom. ii. p. 366.

Fig. 329.

Front view of the skull of the Deer. (From Lond. Coll. Surg. Museum.)

this portion of the bone is compressed, and, in consequence of a central space left unossified (*fig.* 330.), we are enabled to look into

Fig. 330.



Side view of the skull of Moschus. (From a specimen in Lond. Coll. Surg. Museum.)

the orbit of the opposite side; a peculiarity not confined to the animals under consideration, being more marked in certain of the Rodentia and in birds. In Bovidæ the temporal wing of the sphenoid, which is of comparatively large size and much curved backward, does not reach the parietal bone as in the other ruminants; and it is further distinguished by a sharp pointed ridge developed from its anterior margin, which in the preceding genera is only feebly indicated, though tolerably prominent in the Giraffe. The anterior wing extends horizontally forward and is convex on its orbitar surface (*d*, *fig.* 327.). Part of the body of the posterior sphenoid forms, in conjunction with the anterior third of the basi-occipital, two projecting elevations, which are separated from each other by a deep groove: these also appear in the Goats, where they are less marked. In both families the spheno-palatine and the spheno-orbitar foramina are capacious; but in Œgosceridæ the latter openings are somewhat compressed. The *os ethmoides* has the same relations as usual, its cells being greatly developed in the Giraffe.

The *temporal* bone (10), as in other mammalia, consists of three segments. In Camelidæ the zygomatic arches form, in conjunction with the sunken temples and strongly pointed occipito-parietal crests, a striking feature, which imparts to the cranium of this family a carnivorous type of structure. This morphological peculiarity is chiefly noticeable in the Camels properly so called; and in them the glenoid cavity is very deep, being supported in front and behind by prominent apophyses, the posterior of which is united at its base to the tympanic bulla (*fig.* 334.). The latter is much compressed, and also firmly connected above to the paramastoid apophyses of the occipital, leaving a conspicuous cavity between. In the Llamas, at the root of the zygomatic apophysis, there is a large round foramen immediately above the external meatus. In Cervidæ and Antelopidæ the post-glenoid apophysis is feebly developed, and the base of the zygoma is flattened and prolonged backwards toward the occipital crest; the squamous portion is rather extensive and the tympanic bulla of large size. Similar arrangements obtain in the Giraffe, but the zygomatic apophyses are more curved than in the Stags. The base of the zygomatic process in many of the Antelopidæ is pierced by an oval opening, which is situated midway between the external auditory meatus and the glenoid facet; and from it there sometimes proceeds a fissure, which takes an upward direction, to join the parieto-temporal or squamous suture.* This foramen occurs in the Muntjack deer (*fig.* 331.), and, as we have before stated, in the

Fig. 331.

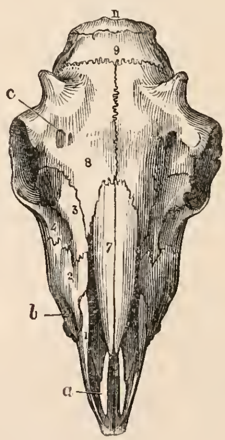
Cranium of the Muntjack. (From Lond. Coll. Surg. Museum.)

Llamas also. In Œgosceridæ the squamous portion of the temporal is comparatively small (*e*, *fig.* 335.), and the tympanic bulla, which is moderately large and somewhat flattened, terminates by a sharp styloid process anteriorly. The post-glenoid apophysis is represented by a very narrow ridge of bone, leaving only a slit-like cavity between it and the meatus. In Bovidæ the temporals (*e*, *fig.* 327.) are partially hid by the overhanging frontals: they develope short and strong zygomatic apophyses; their bullæ (*e′*, *fig.* 327.) are much narrowed, and their styloid processes are divided at the tip into several needle-shaped points.

Bones of the face. — These are more numerous than those of the cranium, and we shall only notice the more important of them in detail.

The *nasals* (7), which vary much in size, are long in the true Camels, a little spread out at the base and deeply notched in front, forming together three salient points: in the Llamas we find them very short and broad posteriorly. In Cervidæ generally, the nasals are much extended lengthwise and bifurcate anteriorly (*fig.* 329.): in the Muntjack (*C. Muntjac*) and in the Giraffe they are particularly wide apart at the upper or posterior border (*fig.* 331.); and in the latter species they exhibit a gradual but marked rising towards the central eminence of the frontals (*fig.* 328.). The naso-frontal suture in the genus Moschus is much denticulated. The nasals are very short in the Eland or Canna (*A. oreas*, Pallas), and in the Moose-deer (*C. alces*, Linn.) In Œgosceridæ and Bovidæ the bones of the nose are moderately long, and slightly convex above in the former (*f*, *fig.* 335.); in the latter family and in the Goats they are divided in front (*f*, *fig.* 327.); but in the Sheep they form together a single V-shaped process (7, *fig.* 332.).

Fig. 332.



Skull of the Sheep, front view. (From Lond. Coll. Surg. Museum.)

The *intermaxillaries* (1) are usually much prolonged, but they do not develope incisive teeth except in the Camelidæ, and a few other species. In the Camels properly so called, and in the aberrant cervine genus Moschus, the outer rami of these bones incline at the superior part almost vertically upwards (*fig.* 334.); but in the Llamas they maintain throughout an oblique direction as obtains in ruminants generally. In both genera they are compressed laterally, and brought round in front, so as to resemble in some measure the beak of a bird; the incisive foramina are remarkably

* F. Cuvier.

small. In Œgosceridæ (*g*, *fig.* 335.) and Cervidæ, for the most part, the ascending rami incline at a very oblique angle, and in Camelopardalis they exhibit a slight concavity at the upper margin. In this last named genus the intermaxillary bones are very long and extremely

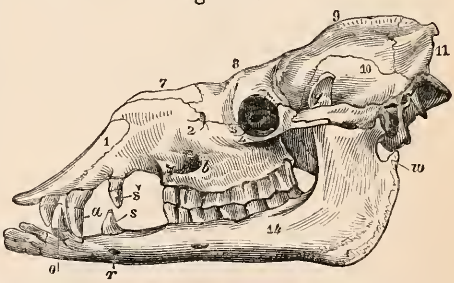
Fig. 333.

Front view of the skull of an Ox, with the right horny sheath detached from the core. (From Lond. Coll. Surg. Museum.)

attenuated at the tip (*fig.* 328.); in Bovidæ, on the other hand, they are of diminished length (*g*, *fig.* 327.), straight, of great thickness and broad in front, giving to the muzzle an aspect characteristic of the group (1, *fig.* 333.). The incisive openings are elongated, capacious, and widely separated in the Giraffe (*fig.* 328.), they are still more so in the Stags (*fig.* 329.) and Antelopes (*fig.* 342.); and in Œgosceridæ and Bovidæ they form enormous clefts, especially in the latter (*fig.* 333.). Several genera have a small free space between the converging points of the intermaxillaries; and this is particularly noticeable in the Giraffe (*fig.* 328). The bones in question are of great length in the Eland or Cape Elk, and in the Moose-deer.

The *maxillaries* (2) usually carry six molars and premolars on either side; exceptions, however, occur in the Camelidæ where one of the premolars is absent, and in this family, as also in the aberrant genus Moschus and in the male *Cervus Muntjac*, canines are developed (*a*, *fig.* 331.). In all ruminants they send processes of greater or less extent to the inner and under part of the orbit, in the situation where these bones lie partly concealed by the jugular or malar bone. As regards the bones themselves there are few other peculiarities worthy of notice; but we may remark, in passing, that in the Giraffe the maxillaries project more than two inches beyond the tips of the nasals. The suborbital foramina (*b*) are placed in the Camelidæ a little before the orbits and above the alveolar ridge, at a point corresponding with the line of juxta-position of the middle and third premolars (*fig.* 334.). In the Giraffe and in other Cervidæ the infra-orbital aperture is seen further forward, on a level with the first premolar: in Œgosceridæ it is on a line with the second (*h*, *fig.* 335.). The Bovidæ have a long suborbital canal opening above the first premolar (*h'*, *fig.* 327.), as in the Stags and Giraffe.

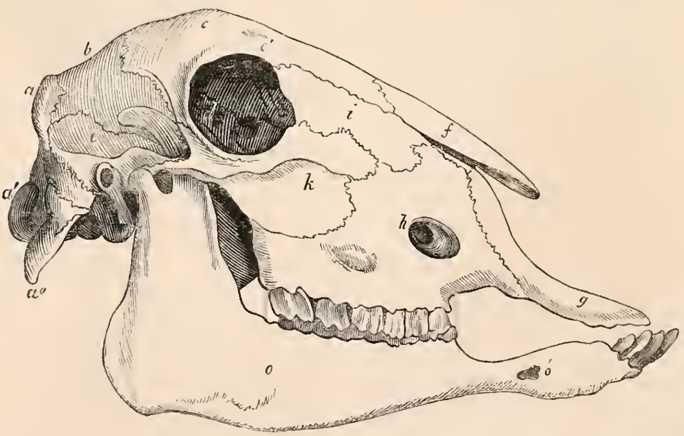
Fig. 334.



Lateral view of the skull of the Camel. (From a specimen in Lond. Coll. Surg. Museum.)

The *lachrymals* (3) are directed forward, and occupy a considerable extent of the cheek; at their point of union with the frontal, nasal, and intermaxillary bones there is usually left a vacant space more or less patent. This space in the true Camels is stated to be of large dimensions; but, out of four *crania* we have examined in reference to this particular, in one only was this opening distinctly visible; in the others the extension of the periosteum, which closes the cavity in front, had ossified, leaving only a few small foramina, irregularly disposed. In the Llama the opening is significant and communicates with numerous sinuses. In regard to the true lachrymal passage in Camelidæ this is represented externally by a single foramen placed directly behind the orbitar ring; but there is in the Camels a second hole which is quite distinct, being connected with the spheno-palatine canal at about half an inch from its orbitar orifice. In Moschus the lachrymal bone is large; it does not articulate with the nasal, and there is no facial cavity: the foramen is close to and within the orbital ring (*fig.* 330.). In Camelopardalis the bone is moderately large and is separated from the nasal in front by an interspace (*fig.* 328.), which, in the single specimen we have dissected, is of a triangular form, and measures an inch and a half in length, and five-eighths of an inch in breadth. According to the experience of Professor Owen this vacant space is invariably present, though not always equally conspicuous. At the orbital ring, midway between the frontal and maxillary lines of articulation, there juts out a small tuberosity, which is bounded on either side by a shallow groove; and from this point the bone is carried downwards and backwards to form, in conjunction with the molar protuberance of the maxillary and the inner border of the malar bone, a shelf-like floor to the anterior half of the orbit. In the specimen just mentioned there exists but one lachrymal foramen, which is of large size, infundibuliform, and situated nearly an inch distant from the anterior border of the orbital ring. In the Stags the lachrymals are hollowed out on the cheek for the reception of the special suborbital glandular apparatus, and they are of large size, but do not touch the nasals, being separated from them by a very extended membranous interspace (*fig.* 329.). In the orbit these bones exhibit relations similar to those indicated in the Giraffe; but there are two foramina, one placed on each side of the lachrymal tuberosity, beneath which they intercommunicate. The possession of "tear-pits," or suborbital sinuses, is not shared by all the Antelopidæ, and in those species in which they do occur the degree of depression in the lachrymal bone is very variable, being in some comparatively shallow, in others well marked: the same observation applies to the open space situated immediately above. Respecting the absence, prevalence, or coexistence of these morphological peculiarities we may, according to M. F. Cuvier, divide this family into three groups: in the first are to be reckoned those which have both a lachrymal depression and a facial interspace, such as is seen in the Gazelle (*A. dorcas*, Pallas), the Stein-boc (*A. tragulus*, Licht.), and the Grys-boc (*A. melanotis*, Licht.); in the second, those possessing the "tearpit," but having no vacant space such as occurs in the genus *Catoblepas*, the Koba (*A. koba*, Ogilby), the Cambing-outan (*A. Sumatrensis*, Desm.), the Chickara (*A. quadricornis*, De Blainv.), the Caama (*A. caama*, Cuv.), and the Bubale (*A. bubalis*, Pallas); in the third, those having the interspace, but no depression, such as takes place in the Reh-boc (*A. capreolus*, Licht.), the Chamois (*A. rupicapra*, Pallas), the Canna (*A. oreas*, P.), and the Nil-ghau (*A. picta*, P.). The Œgosceridæ have the lachrymals very large and of great length, this being especially the case in the Sheep, where they articulate with the bones of the nose (*i. fig.* 335.). The Goats have usually a small open space on the cheek, both of the above genera being provided with a small tubercle at the anterior margin of the orbit. The foramina are placed within the ring and are remarkably large in the Sheep. The lachrymals in Bovidæ are of still greater size, and very conspicuous (*fig.* 327.); they develope prominent antorbital

Fig. 335.



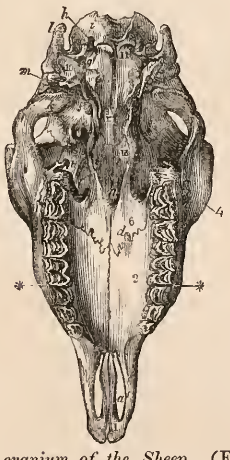
Skull of the Sheep, viewed laterally. (From Cuvier.)

tubercles and have the connecting sutures on the face marked by deeply toothed interlineations. There is no membranous interspace, and the foramen, which is funnel-shaped, is situated at the margin of the orbital ring immediately behind the tubercle.

The *malar* or *jugular* bones (4) do not offer any very striking peculiarities. They are bulky and strong in the Camelidæ, and of great breadth below the orbit: in the Llamas they advance further forward upon the cheek than in the true Camels, and the zygomatic apophyses are very short. In Moschus the post-orbitar apophysis is of considerable size—that of the zygoma somewhat narrower (*fig.* 330.). In Antelopidæ and Cervidæ generally, the malars are slender, and have short zygomatic apophyses: this latter feature is especially noticeable in the Giraffe. They are broad and of great thickness in Œgosceridæ (*fig.* 335.), in which family and in Bovidæ they are much prolonged upon the cheek, in the latter being a little bifurcate anteriorly at the maxillary line of suture (*fig.* 327.).

The *palatines* (6) are largely developed. In Camelidæ, where the roof of the mouth is very long, the palatal laminæ have a great longitudinal diameter; in the Llamas the transverse suture extends to a level with the anterior border of the first true molar; the central palatal cleft, which is angular, reaches the front margin of the middle or second true molar, while the lateral notches proceed as far only as the anterior border of the last molar. In Cervidæ the palatals occupy a large square space at the inner and lower part of the orbit, but this is not the case in the Giraffe, where this part of the bone is rather smaller and lies partly concealed by the shelf-like process of the lachrymal and the molar prominence of the maxillary bone. The lateral fissures at the guttural margin of the palate are very wide in this family and extend deeper into the roof of the mouth than does the mesial cleft. These three clefts are placed in the Giraffe nearly on the same level, the central fissure having a semicircular outline. In the Muntjack deer the two lateral notches are much in advance of the mesial cleft. The guttural portion of the combined palatines in Œgosceridæ is of great breadth, and the fissures, which are not very deeply notched, are all very nearly on the same level (*n*, *fig.* 336.): the orbitar or

Fig. 336.



Base of the cranium of the Sheep. (From Lond. Coll. Surg. Museum.)

ascending plates are large and square, but deficient at the upper part, where there intervenes a space or hole analogous to the spheno-palatine foramen. This opening is particularly capacious in the Sheep. In Bovidæ the palatines occupy about a fourth part of the oral roof: the ascending or suborbitar portions, which are of enormous bulk, are almost entirely hid by the lateral overlapping of the posterior border and supra-molar prominences of the upper jaw; the palatal notches are very deep, especially the two lateral, which are remarkably broad and somewhat in advance of the mesial.

The *vomer* and *ossa spongiosa seu turbinata*, in consonance with the general extension of the facial bones in ruminants, are chiefly particularised for their longitudinal development. In the orbits the wings of the vomer are represented by very small laminæ, which appear at the upper border of the opening corresponding to the spheno-palatine foramen. In certain of the Stags the azygos portion descends between the pterygoid apophyses of the sphenoid to a level with the palate, dividing the mesial fissure in two and contributing to form in this region a backward expansion of the oral roof. The spongy bones will be referred to when describing the organ of smell.

The *inferior maxilla* or jaw-bone proper is of great length; in which respect it follows the course of the bones of the upper jaw. Between the canine and first premolar of either side there is in the typical ruminant, an extended interval, at which part the body is constricted; and immediately in front of the mental foramen (*r*, *fig.* 337.) it again ex-

Fig. 337.

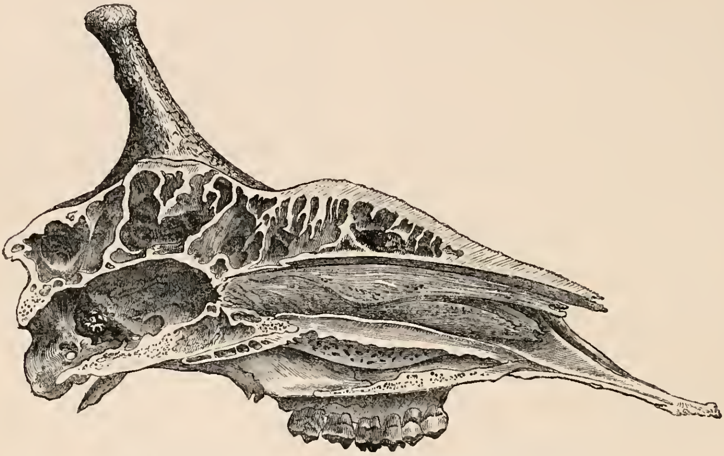
Jaw-bone of the Sheep. (From Lond. Coll. Surg. Museum.)

pands toward the alveolar margin to give support to the teeth. The angle of the jaw is prominent and rounded posteriorly; in this situation also it is comparatively thin and broad, as in Solipeda. The coronoid processes of the rami (*g*, *fig.* 337.) are particularly long curved backward, and a little hooked at the summit. The glenoid apophysis is short, and the facet flat and slightly concave, to admit of free lateral motion on the wide convex articular surface of the temporal zygoma. The sigmoid notch is shallow. In the Camel there is an additional process at the parotid border (*w*, *fig.* 334.), analogous to the similar but more marked apophysis in Carnivora.

Cranial peculiarities. — Under this head we proceed to notice certain arrangements requiring further attention, and in the first place the remarkable sinuses which exist in the skull of the Giraffe. Though these be nothing more than an extension of the ordinary frontal, ethmoidal and sphenoidal cells, yet their significance is not the less apparent or important when considered in a physiological or teleological point of view.

It has been considered necessary to preserve the cranium of the Giraffe at present in our possession entire; consequently, we are unable to offer any account of these sinuses from personal examination, which is the less to be regretted, as Prof. Owen has placed

Fig. 338.



Sectional view of the cranium of the Giraffe. (From Owen.)

on record the following description of this structure*; "The part of the skull to which the elastic ligament is attached is raised considerably above the roof of the cranial cavity by the extension backwards of large sinuses, or air-cells, as far as the *occiput.* The sinuses commence above the middle of the nasal cavity, and increase in depth and width to beneath the base of the horns, where their vertical extent equals that of the cerebral cavity itself. The exterior table of the skull, thus widely separated from the vitreous table, is supported by stout bony partitions, extended chiefly in the transverse direction, and with an oblique and wavy course. Two of the most remarkable of these bony walls are placed at the front and back part of the base of the horns, intercepting a large sinus immediately over the middle of the cranial cavity, and from a third and larger one behind. The sphenoidal sinuses are of a large size."

Slight differences in the development of the cranium are found in Giraffes inhabiting respectively the more northern or southern regions of Africa, these peculiarities having especial relation to the position and approximation of the horns. In the Abyssinian specimen (about two years old) dissected by us, several particulars were noted, a few of which are here selected †: —

	Inches
Length of cranium - - - - - -	19
Breadth between orbits - - - - -	8¾
Incisive angle to central eminence - -	11½
Length of horns - - - - - -	5½
Distance between horns at the base - -	0½
Depth of orbit - - - - - -	3
Diameter of orbital ring - - - - -	2½
Breadth of occipital condyles - - -	3⅞
Vertical depth of each condyle - - -	2½
Length of lower jaw - - - - -	15½

In this list will be remarked the extreme elongation of the bones of the face, as shown by the distance of the incisive angle from the central prominence—the great depth of the orbits—the narrow space between the bases of the horns — the length of the jaw—and more particularly the extended vertical diameter of the condyloid facets of the occipital bone. The elongation of these articular surfaces in the direction indicated, permits of the head being drawn into a line with the neck, and Prof. Owen states, from observing this action in the living animal, that he has seen it stretched backward beyond this line.

Horns. — In the Giraffe we have a unique example of solid persistent horns, completely invested with a hairy integument. They are placed on two bony elevations, having a position analogous, in some respects, to that of the osseous cores of the Stags; but, being separated from them by a synchondrosis, they are to be regarded as independent developments or "epiphyses" and not "apophysial" outgrowths (*fig.* 328.). As has been already observed, the protuberances are formed in part by the parietal and frontal bones, the

* Memoir on the Anatomy of the Nubian Giraffe, Zool. Trans. vol. ii. p. 235.

† Dr. Cobbold, On the Anatomy of the Giraffe, Annals of Nat. Hist. for June, 1854.

coronal suture passing transversely across the centre of each osseous expansion, from side to side. The bones are easily detached by maceration (at least in the younger animal), and when withdrawn, there is brought into view an intervening sheath-like periosteum, which can also be separated from the concavity at the base of the horn. This cup-shaped hollow, owing to the columnar disposition of the osseous laminæ, and the very numerous perforations for the passage of nutrient vessels, presents the appearance of a sieve, depressed into a conical form. Both in the Cape and Nubian varieties a sexual difference obtains in reference to the extent to which the horns are developed. In the male adults they are larger and more closely approximated at the base than in the females, and, according to Prof. Owen's observations on the horns of the Cape Giraffe, "their expanded bases meet in the middle line of the skull, so that they would entirely conceal the coronal suture even if it were not early obliterated in this sex."* The basal portions of the horns in the females are widely separated. In our specimen (a Nubian male). the internal and lower margins of the horns remain, severally, half an inch apart, and the interfrontal suture is still distinct throughout its entire length. In regard to the asserted existence of a third horn surmounting the anterior central protuberance, an examination of the cranium, above alluded to, only serves to confirm the extended observations and conclusions of Prof. Owen on this subject. We have shown that this elevation is due to an enlargement of the subjacent frontal sinuses, and in this respect it resembles the posterior horn-shaped apophyses. It must be remarked, however, that although, in our example, there is no superimposed osseous deposit, there is, nevertheless, a cartilaginoid thickening of the periosteum in that situation; this, we can readily believe, might constitute a nucleus favourable to the formation of an epiphysis similar in all respects to the true horns lately described. We have not had an opportunity of inspecting the crania in the museum of the Royal College of Surgeons, London, but, through the kindness of Dr. Ball, have examined the skeleton of a male Giraffe which died (during sexual excitement) at the Dublin Zoological Society's Gardens, and which is now preserved in Dr. Harrison's Anatomical Museum. In this individual the central cranial eminence is not smooth as in our specimen; on the contrary, it is particularly rough, owing to the deposition of osseous nodules, which bear a marked resemblance to the irregular bony laminæ prolonged from the attenuated margins of the bases of the true horns. If these rough prominences could be shown to be separable by maceration, we might with good reason infer the rudimentary existence of a third horn; if, on the other hand, they are merely exostoses or outgrowths (and to this opinion we incline), we think their deceptive aspect offers, in some measure, an explanation of the incorrect description of this structure recorded by Cuvier, and the inaccurate figure given by Rüppell.*

* Memoir, *loc. cit.*

The deciduous branching horns of the deer present two well-marked morphological types, — one group possessing rounded antlers, and the other having them more or less flattened and palmated. Of the former, characteristic examples are seen in the horns of the Roebuck (*C. capreolus*) and Red Deer (*C. elaphus*), — and of the latter, in the Elk (*C. alces*) and Fallow Deer (*C. damas*). The remarkable periodical development of these cranial outgrowths is most interesting in a physiological point of view, and both types of structure exhibit the same general law of increase. The male calf of the Red Deer at the sixth month differs from the female of the same age, in having two small elevations or "bossets," which represent the first indication of horns. These processes acquire, in the second year, the form of simple unbranched stems or "dags" (*a*, *fig.* 339.), at which date the deer

Fig. 339.

Development of the horns in the Red Deer. (From Cuvier.)

is designated a "brocket" by the English, and by the French a "daguet." The dagger-like horn being shed, its place is occupied in the third year by another, carrying usually one, but sometimes two, and even three branches or "tynes" (*b*, *c*); in this condition he is called a "spayard." The horn of the fourth year assumes a more complex aspect (*d*, *e*), and the summit or "crown" of the stem begins to spread and divide; at this stage he is styled a "staggard." At the fifth year there are five or six branches, and at this period he is termed a "stag." At and after the sixth and seventh years the number of "tynes" is very variable, and the growth of the horn being now perfected, the individual is technically denominated a "hart" (*f*). The palmated horns of the Fallow Deer exhibit similar gradations of development. At the second year the "buck-fawn" or

* Atlas zu der Reise in Nordlichen Afrika, von Edouard Rüppell, Pl. 9. Since the above was written Prof. Quekett has politely afforded us an opportunity of inspecting the *crania* in the Hunterian Collection. The osseous nodules noticed in the Dublin specimen not only exist in one of these crania, but they could be partly raised from the subjacent bone by the easy insertion of the finger-nail under the margin.

"pricket" puts forth a simple "dag" or cylindrical shaft (*a*, *fig*. 340.), which is slightly bent forward. In the third year the branching commences, and he is said to be a "sorel" (*b*). The antlers in the fourth year grow more numerous, and the stem is bifid at the summit (*c*); at this period the Fallow Deer is

Fig. 340.

Development of the horns in the Fallow Deer. (From Cuvier.)

entitled a "sore" by sportsmen. After this date the upper part of the brain or shaft becomes more palmated, and irregular serrations or "snags" are produced at the margin (*d*); the animal is now a "buck of the first head," and, as age advances, the snags enlarge, and take on, more or less, the appearance of true antlers. In the Rein Deer the horns undergo a similar metamorphosis; they are of great size in both sexes, but are somewhat less branched and slender in the female; the brow-antlers are much prolonged forward over the forehead.

The nature of the anatomical change which takes place in the adult individual during the periodical renewal of the antlers, is characterised by, and contemporaneous with, the following phenomena; — a strong determination of blood to the head takes place at the spring of the year, and the vessels surrounding the frontal apophyses enlarge. This increased vascular action results in the secretion of a fibro-cartilaginous matrix, manifesting itself externally by a budding, commencing at the summit of the "core," at the spot where the horns of the previous season had separated. In the early condition the horn is soft and yielding, and it is protected only by a highly vascular periosteum and delicate integument, the cuticular portion of the latter being represented by numerous fine hairs, closely arranged. From this circumstance the skin is here termed the "velvet." As development goes on, a progressive consolidation is effected, — the ossification proceeds from the centre to the circumference and a medullary cavity is ultimately produced. While this is taking place a corresponding change is observed at the surface. The periosteal veins acquire an enormous size and by their presence occasion the formation of grooves on the subjacent bone. At the same time osseous tubercles, of ivory hardness, appear at the base of the stem; these coalesce by degrees and enclose within their folds the great superficial vascular trunks, which are thus rendered impervious. The supply of nutriment being cut off, the first stage of exuviation is accomplished by the consequent shrivelling up and decay of the periosteal and integumentary envelopes. The full growth of the horns is now consummated, and the animals, being aware of their strength, endeavour to complete the desquammation by rubbing them against any hard substances which may lie in their path; this action is technically termed "burnishing." After the rutting season the horns are shed, to be again renewed in the ensuing spring.

The disposition of the horns is invariably symmetrical in a state of health, but the antlers are sometimes disproportionate on either side and their growth incomplete from deteriorating circumstances. A remarkable sympathy exists between the generative organs and the horns, and any imperfection in the one induces a corresponding change in the other. In consequence of this reciprocal influence, the development of the horn may be arrested and the periodical shedding prevented by castration. An illustration of this is to be seen in the cranium of a Fallow Deer preserved in the College of Surgeons' Museum, London. The horns of ruminants are seldom more than two in number, but exceptions occur in the case of the extinct Bramatherium and gigantic Sivatherium (*fig*. 341.) found in the tertiary deposits of Northern

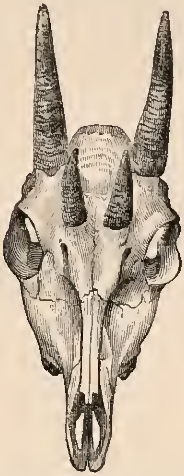
Fig. 341.

Front view of the cranium of the Sivatherium. (From a model in the Lond. Coll. Surg. Museum.)

India. Living instances of more than a single pair are seen in the Four-horned Goat and Many-horned Sheep; also in the Jungliburka Antelope (*A. subquadricornutus*) where the anterior pair are rudimentary, and in the Chousingha (*A. quadricornis*), several species of which have been described by authors (*fig*. 342.).

The structure of the horn in Cavicornua is exceedingly simple. The frontal "apophyses" or "cores," instead of branching, form cylindrical shafts, more or less solid, the surface being protected by the ordinary periosteum, and by an extension of true skin, the cuticular portion of which is developed into a dense horny sheath (*fig*. 333.). If a transverse section be carried through the base of the "core," a number of cavities will be exposed, which are continuations of the frontal sinuses. These spaces do not exist in certain of the antelopes, as for example in the Gazelle (*A. dorcas*) and the Sasin (*A. cervicapra*). The horns exhibit a great variety of curvature and outline, and in those of the Cabrit or Prong-horn Antelope (*A. furcifer*), we have an approach toward the cervine type. The prong is situated about half way up, and may be considered as analogous to the brow-antler; immediately below it the root is rough, scabrous, and nodulated, being covered also by a hairy integument (*fig.* 343.).

Fig. 342.



Front view of the cranium of the Chousingha. (From a specimen in Lond. Coll. Surg. Museum.)

Fig. 343.

Horns of the Cabrit. (From a specimen in Lond. Coll. Surg. Museum.)

In the Buffaloes the horns acquire a prodigious size, and the cuticular sheath forms, in some instances, a thick envelope over the entire forhead.

Vertebral column and bones of the trunk. — Considerable disparity prevails in the length of different portions of the spine, depending upon the comparative elongation of the individual bones, and not upon their number. The following table, selected from Cuvier, illustrates the trifling deviations in a numerical point of view, — the seven cervicals being added and indicated in the totals: —

	D.	L.	S.	C.	TOTALS.
Camel - -	12	7	4	17	47
Vicugna -	12	7	5	12	43
Moschus -	13	6	3	14	43
Red Deer -	13	6	4	16	46
Giraffe - -	14	5	4	18	48
Gazelle - -	13	6	4	14	44
Chousingha -	13	5	4	14	43
Goat - -	13	6	4	12	42
Sheep - -	13	6	4	16	46
Ox - -	13	6	5	18	49

In Camelidæ the bodies of the vertebræ of the neck are much lengthened (*fig.* 323.), but it is in the Giraffe (*fig.* 345.) that we see the most remarkable conformity to the cervical type in this respect. The spinous processes of this division of the column are lessened in all mammiferous animals in proportion to the length of the cervix, and therefore we find them in the above mentioned ruminants almost entirely effaced (except in the seventh vertebræ) to admit of free motion backward. This action is further facilitated in the Camels and in the Giraffe by the ball and socket-like conformation of the articular ends of each vertebral body, as pointed out by Profs. De Blainville and Owen. The anterior extremity of the "centrum" is convex (*fig.* 344.), and the posterior concave, but there is no intervertebral synovial apparatus as seen in reptiles. The transverse processes in the short-necked typical ruminants are compressed, and form double "apophyses" on either side. The anterior or inferior pair are directed forward, and the posterior or superior project laterally, their common expanded base being pierced for the passage of the vertebral artery. In the latter particular, a similar arrangement obtains in the Giraffe, but the openings are placed nearer the spinal canal, because the transverse processes are feebly developed, as in all other long-necked ruminants. The Camels and Llamas do not exhibit the perforation in question. In them, the vertebral arteries enter the posterior opening of the great neural canal, external to the dura-matral sheath, and in this position they are partly lodged in a groove at the base of the superior lamina. At the anterior part of the bone this channel becomes arched over for a short space, and converted into a distinct passage

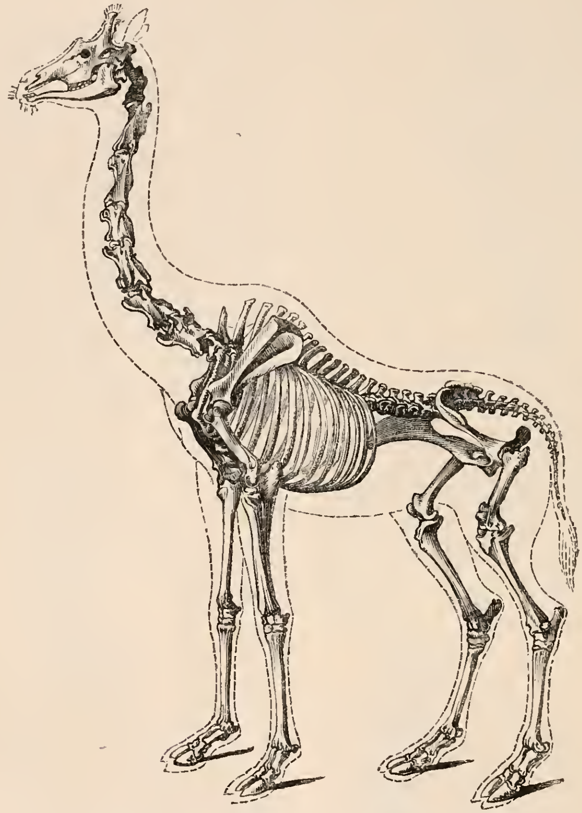
Fig. 344.

Section of the cervical vertebræ of the Camel. (From Coll. Surg. Museum.)

(*fig.* 344.). The *atlas* in the Camels is not thus modified. In all other ruminants, including the Giraffe, an opening exists in this bone, which is placed at the fore part of the superior ring. The odontoid process of the *axis* or *dentata* is well marked and prominent in the short-necked ruminantia, but the Giraffe and Camels have it very small and incorporated with the articular end of the body; in them, also, very slight traces of transverse "apophyses" are detectable.

The *dorsal* vertebræ are distinguished for the great length and development of their spinous processes. The latter have an extraordinary elevation in the Giraffe, for the attachment of the powerful *legamentum nuchæ*, which is broadest at this point (*fig.* 345.). The spinous "apophyses" are large in the Bovidæ, and still more bulky in Camelidæ. The transverse processes of the *lumbar* vertebræ in the first-named family are extremely prominent, and have a straight lateral direction. In the swift-bounding Stags and Antelopes they are shorter, and a little curved forward. In Camelidæ they are largely developed, slightly bent downward, and abrupt at their extremities, the last pair being comparatively short and narrow. The *sacrum* consists of three, four, or five pieces consolidated together, to the anterior of which the *ossa ilea* are articulated. The spinous processes form a single continuous crest. The *caudal* vertebræ vary in number, and, in the foregoing table, eighteen are assigned to this region in the Giraffe. Prof. Owen has counted as many as twenty in the Nubian variety. The Llamas, Stags, Goats, and certain of the Antelopes have the tail short, with a proportionate diminution of bony segments; this appendage is of considerable length in the true Camels, the Gnus, the Oxen, and some of the Sheep.

Fig. 345.



Skeleton of the Giraffe. (From Pander and D'Alton.)

The *ribs* vary chiefly in respect of their size. The Giraffe has seven directly united to the sternum, and an equal number unattached. Eight are true and five false in the Stag, and the same division occurs in the Ox. They are strong in the true Camels and in the Giraffe, being particularly broad toward the sternal ends. The same peculiarity holds good with most of the bovine species. In the Camel seven pairs are connected to the sternum, the anterior ones being straight and short; five remain unsupported. The ribs are very narrow in the Bison, and particularly slender in the Antelopes and Deer. The *sternum* is flattened in ruminants, its first bone being rounded in front, and somewhat attenuated. This is especially the case in the Giraffe, where the breadth increases towards the posterior border, at which point it is extremely thick. It is more or less curved in the Camel and Giraffe, particularly in the latter. We have observed in the skeleton of an Arabian Camel, preserved in the Edinburgh College of Surgeons' Museum, that the second bone of the sternum is of very great bulk, while the first is small and flat anteriorly.

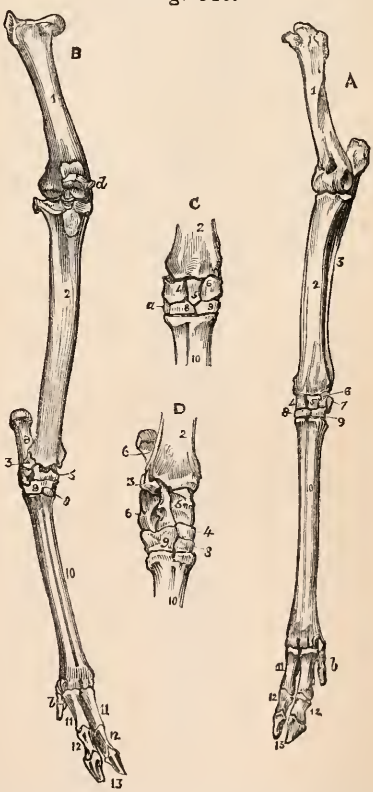
The *pelvic bones* are broad and strong in the Camels and bovine tribes, and comparatively slight in the Antelopes and Deer. In the Giraffe and in the Camelidæ the crest of the ileum is rounded, the neck long, and the upper surface of the bone concave. The ileum is extremely prominent and large in the Ox and Buffalo, and in respect of the neck, acquires an almost vertical position; the prominence of the ischium is placed on a higher level than the cotyloid cavity. In ruminants generally, the posterior angle of the ischium presents the appearance of a tripod. The ischiatic notch is deep. In Œgosceridæ, Cervidæ, and Antelopidæ, there is a depression immediately in front of the cotyloid cavity for the insertion of the tendon of the straight muscle of the thigh. In Moschus, according to M. F. Cuvier, the sacro-ischiatic ligament and connecting aponeuroses ossify, in consequence of which there is formed in this region a shield-like osseous plate extending from the crest of the ileum to the ischial tuberosity.*

Bones of the anterior extremity. — There are no traces of a *clavicle* in this order. The *scapula* is long, and has the form of an isosceles triangle, the base of which is represented by the spinal border, and the apical angle by the glenoid facet. In Camelidæ the spine of the bone is prolonged downwards over the neck, forming, in this respect, an approach to the pachydermatous type. The acromion apophysis is likewise developed in Bovidæ; but it can scarcely be said to exist in other ruminants. In every division of the family we find the neck of the scapula much elongated, and the extreme manifestation of this peculiarity in the Giraffe, together with a nearly vertical direction of the bone, produces the remarkable elevation of the shoulder, characteristic of that animal. The coracoid process exists only in a very rudimentary condition, or is altogether absent. The relative disproportion between the supra and infra-spinal spaces is very striking; usually the former consists only of a narrow plate of bone, but its development in the Camel is more cogent. In Bovidæ the root of the spine is blended and continuous at its acromial end with the anterior scapular border.

The *humerus*, according to its thickness and bulk, affords a very fair criterion of the comparative activity and strength of the different species. In Camelidæ and Bovidæ this bone is very massive, and the tuberosities are of great size, the lesser prominence being more elevated than the greater in the first of these two tribes, and hollowed out in front by a capacious channel. The linea aspera stands out boldly, and the external and internal condyles are drawn back, as it were, to deepen the olecranon cavity. The trochlear grooves and ridges are also well marked. The foramen for the passage of the nutritious artery is generally situated at the commencement of the lower third of the bone; but a slight variation is occasionally observed. Thus, in regard to its position in the Giraffe, Professor Owen states that the "medullary artery enters the bone at its inner side about the junction of the upper and middle third," while it is added, that in the skeleton preserved in the Museum of Comparative Anatomy at Paris, the vessel enters the *left* humerus at the point of union of the middle and lower third.* We have found a similar disposition to occur in our example. The foramen enters at the posterior and inner surface of the right humerus, and is situated very near the centre of the shaft; but in the bone of the left side it is placed further down, as in the Parisian specimen: the opening is likewise rather smaller.

The *bones of the forearm* (*fig.* 346., A. 2, 3) are

Fig. 346.



Bones of the fore and hind limbs of the Deer. (From Lond. Coll. Surg. Museum.)

* For details, see Art. "Pelvis."

* Memoir, *loc. cit.*

intimately united, and, being connected to the humerus by a simple hinge joint, are always retained in a state of pronation — as the surface corresponding to the palm of the hand is always directed backwards; to increase the steadiness and strength of the limb, the upper end of the ulna is very thick, and in the upright position of the animal the articular angle of the olecranon is firmly locked between the brachial condyles. There is a deep groove indicating the radio-ulnar line of union, at the upper part of which is a vacant space, and another is sometimes present near the distal end. In certain individuals the ulna is represented by two distinct pieces, the central part of the shaft having disappeared. In all cases the olecranon is extremely prominent, and the bone is relatively much longer than the radius. There is no vacant interval between the bones in the Camel, which together acquire an extraordinary length. The radius and ulna in the Javanese musk are nearly of equal bulk, and the line of attachment is very distinct throughout. In a specimen preserved in the Edinburgh College of Surgeons' Museum, the bones of the right side are anchylosed only at the middle of the shaft.

All ruminants possess six *carpal bones* (A. *fig.* 346.), and some have seven, which are disposed in two rows. In the upper may be recognised the *os scaphoides* (4), *os lunare* (5), *os cuneiforme* (6), and *os pisiforme* (7); in the lower the *os trapezoides* (8) and *os magnum* (9), and in the Giraffe and Camel the *os unciforme* (C, *a*.).

The *metacarpals* are represented by a central *cannon* bone (10), and in the Deer-tribe and Antelopes by two additional rudimentary splint-like pieces, which are separated from the lower and back part of the former by the intercalation of four *ossa sessamoidea*.

Fig. 347.

ection of the cannon bone. (From Lond. Coll. Surg. Museum.)

The large central shaft or cannon is in reality composed of two metacarpals, as can be readily demonstrated by making a longitudinal section, such as is displayed in the annexed woodcut (*fig.* 347.). In this view the duplicity of the shaft is shown by the thin lamina of compact osseous tissue (*d*), traversing the hollow cylinder from end to end; and its duality is further evinced by the bifid character of the distal extremity (*a*, *b*), as well as by a deep median furrow at the posterior surface. The two splint bones are homologous with the metacarpals of the index and little fingers in the human subject. They are not present in all ruminants; but in the Deer they attain a considerable size, and support two small digits. In some cervine species these styliform metacarpals are seen attached at both extremities of the cannon bone. In the genus Moschus they are as long as the shank, forming thus a transition towards the four-toed pachydermata.

Six *phalanges* enter into the composition of the cloven foot, the two upper being the longest, and having a position analogous to the pastern bone of Solipeda; the superior articular surfaces are deeply grooved for the reception of corresponding ridges (*fig.* 347. *c*, *c*), surmounting the trochlear facets of the cannon bone. The second pair are short, the distal end presenting an extended convex plane for the hinge movement of the ultimate phalanx. A sasamoid bone is sometimes seen behind this joint. The last pair are more or less triangular, and their combined plantar surfaces form a semicircular disc, resembling that of the coffin bone of the Horse. In those genera which have supernumerary digits, the rudimentary phalanges do not, under ordinary circumstances, reach the ground; and though invested with a hoof-like covering, they can but slightly aid in supporting the weight of the body. In the Rein-deer, however, as Sir Charles Bell observes * "these bones are strong and deep, and the toe, by projecting backward, extends the foot horizontally, thus giving the animal a broader base to stand on, and adapting it to the snows of Lapland, on the principle of the snow-shoe." The same observation applies, though in a more limited sense, to those species where the lateral toes are less conspicuously developed, in which case the elasticity and firmness of the spring will be heightened when bounding through weedy thickets and on grassy moors.

Bones of the posterior extremity. — The hind and fore limbs are not of equal length, and if the actual extent of the individual bones be added together, the balance will be found in favor of the posterior limb. This is evident at a glance in the genus Moschus, and in the Giraffe there is no exception to this rule. In order to make our position clear, the following relative admeasurements are deciphered from personal examination: —

* Bridgewater Treatise, "On the Hand," p. 93.

	Fore limb.	Hind limb.
Dromedary - - - -	62 inches	65 inches
Javanese Musk - -	7½ "	11 "
Red Deer - - - - -	31 "	38 "
Rein Deer - - - - -	32 "	39½ "
Fallow Deer - - - -	27 "	34 "
Irish Elk - - - - -	51 "	60 "
Goat - - - - -	19 "	24½ "
Ox - - - - - - -	38 "	48 "

It will be remarked that the proportionate difference, as here indicated, is much less in the Arabian camel than in the more typical ruminants.

The *femur* (*fig*. 346. B. 1) resembles for the most part that of other mammifera, being characterised by a rather short shaft and neck, and having the head placed nearly in a line with the longitudinal axis. The great trochanter is prominent, and forms the highest point when the limb is placed in an upright position. The inter-trochanteric fossa is capacious. The bone presents at the inferior end an extended articular surface, and bulges at the forepart, where it is deeply grooved for the patella and tendon of the quadratus muscle. Behind the external condyle is a hollow, and its rough outer margin is continuous with the faintly indicated linea aspera. In the Giraffe the distal extremity of the thigh-bone attains a prodigious development. The nutritious artery enters at the anterior aspect of the cylinder a little below the cervix, as in other keratopherous ruminants; we have also observed the arterial foramen of the left side to be about half an inch lower than on the right, an arrangement analogous to the deviation noticed in connection with the humerus of this species.

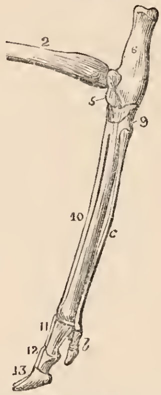
The *patella* (*d*) is comparatively small and compressed laterally; it is sharp in front, and the applied surface exhibits two well marked facets.

The *tibia* (2) is the longest bone of the hind leg, and is chiefly remarkable for the prominence of its spine, which projects from the upper fourth of the shaft and presents a sharp ridge directed outwards. A long styliform *fibula* is stated to exist in Moschus, which is united to the external border of the tibia. In the Javanese Musk preserved in the Edinburgh College of Surgeons Museum, there is no appearance of this bone. Slight traces of the fibula, however, are met with in other cervine genera, in the form of small osseous nodules jutting from the head of the tibia, and in some of the Deer tribe there is likewise to be noticed a small bone constituting the external maleolus (*fig*. 346, D A. 3). This supplementary piece is, in all probability, the representative of the lower end of the fibula, and it is articulated by three distinct facets to the tibia, os calcis, and the astragalus.

The bones of the tarsus, properly so considered, are five in number, viz.,—*os calcis*, (2) and *os astragulus* (5), two *ossa cuneiformes* (8), and a single mass (9) resulting from the union of the *os scaphoides* and *os cuboides*. In the Giraffe and in certain Antelopes and Deer the two cuneiforms are conjoined. The bone of the heel is in all much elongated. In Camelidæ the scaphoids and cuboids (D 4 and 9) are disconnected.

In conformity with the disposition of the metacarpal bones in the anterior limbs, the *metatarsals* form a single cannon bone posteriorly (10). More evident traces of original duplicity are observable in the latter, than in the corresponding cylinder of the fore-limb, owing to the presence of a furrow in front in addition to the one placed behind; the latter groove being moreover particularly deep. In Cervidæ and Antelopidæ, splint-bones homologous with the metatarsals of the second and little toes of the human subject are occasionally present, to support two supernumerary digits as obtains in the fore-leg; but these spurious phalanges are sometimes seen without the styliform appendages. In Moschus the rudimentary metatarsals acquire a much greater significance, extending upward nearly as far as the tarsus (*c*, *fig*. 348.). We have already alluded to a similar peculiarity in the metacarpus of this aberrant genus. The disposition of the true digital phalanges and their accompanying ossa sessamoidea simulates in every respect that displayed in the construction of the cloven foot of the anterior extremity.

Fig. 348.



Bones of the hind limb of Moschus. (From Lond. Coll. Surg. Museum.)

Myology.—The muscles of ruminants exhibit few peculiarities apart from those of quadrupeds generally. They present arrangements very similar to those seen in Solipeda, and in the article devoted to the consideration of that group, numerous comparisons have been instituted in reference to the more important myological deviations found in this order. Selecting principally the Ox and Sheep as types, we have to offer, in regard to this great system of motary organs, the following particulars :—

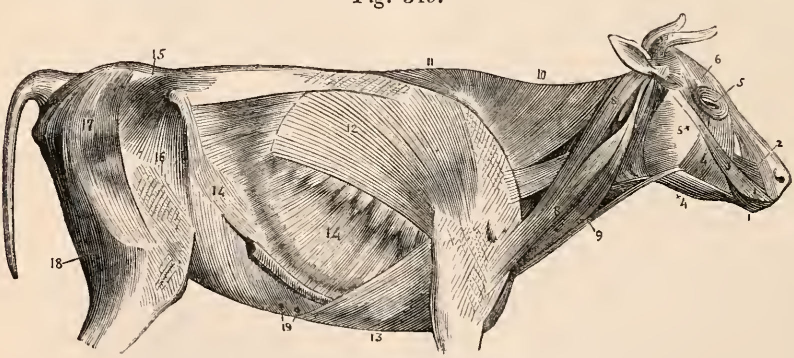
Panniculus carnosus.—Traces of this superficial muscular investment exist over the whole surface of the trunk, but in certain localities the fibres are more cogent, and form separate bundles, so as to assume more or less the character of distinct muscles. Eight or ten such bundles may be remarked in different species. In the first place we have a broad band extending from the fore-part of the neck, and spreading toward the lips and forehead; this constitutes the *musculus cutaneous faciei.* Again, it is very strongly marked at the neck, especially in the Sheep; here it is denominated the *m. cutan. colli.* In other domestic animals of the non-ruminant kind, such as the Dog, Cat, and Pig, this second division of the fleshy envelope is still more striking. Over the shoulder of the Ox there is a third layer of thickened fasiculi (*m. cutan. humeri*); and lastly, we find a highly developed mass, taking its origin from the fascia lata of the thigh immediately above the patella, and proceeding forward, the fibres radiate toward the scapula in front and the abdomen below; this is the *m. cutan. maximus seu abdominis.* The insertion of the panniculus is directly into the skin, which everywhere covers it, and "on this texture it can alone act, seeing it is completely isolated from the deeper seated parts, by an universal layer of fascia, which thus enables it to slide more freely upon them. When in action, the fibres throw the skin into folds that form right angles to their general course; the chief points from which they act being the angle of the jaw, the scapula, the patella, and the pubis." * The principal function appears to be that of serving as an instrument of defence. By its action animals have the power of jerking and shaking the skin, thus removing irritating matters, — also of erecting bristles and spines as instanced by the defensive armature of the Hedgehog, — and in aiding the process of lactation, as obtains in the Marsupiatæ. Were it not for the constant and involuntary action of the muscle, the torture (to which many animals, particularly cattle, are subjected, from the stings and bites of flies and other insects), would become intolerable, and consequently we find in those creatures which are most exposed to their injurious attacks a preponderating development of this structure.

In the same category as the above cutaneous muscles may be associated the *musculus preputialis seu umbilicus*, the superficial *orbicularis palpebrarum*, and certain of the complicated set of organs which act upon the concha and scutum of the external ear. Of the latter, sixteen pairs have been described as common to the Ox, and nearly as many have been indicated in the Sheep. In both genera they surround the ear on all sides, and offer similar characters in respect of relative size and position. By their reciprocal action the auricular appendage is turned in every direction, as well as rotated upon its own axis; it is likewise expanded and contracted by such of them as proceed from one part of the concha to another. The orbicular muscle of the eyelid (5, *fig.* 349.) is thick and fleshy, and its action is aided above and below by thin strata of fibres coming from the panniculus; these are independent of the ordinary elevators and depressors of the lid.

Muscles of the head and trunk. — Referring to the accompanying figures for a general outline of the superficial and deep muscular layers included in the above division, we propose to treat in detail of such muscles as acquire a particular interest in respect of their position or importance in a physiological point of view.

In the clavicle-bearing mammals the *trapezius* consists of two parts, — an anterior or clavicular portion, and a posterior or scapular division; but in ruminants and other quadrupeds which are unprovided with these bones, the posterior section is alone represented by the trapezius properly so called (10, 11, *fig.* 349). On this account it is comparatively small and restricted in its superior attachments, the fore-part being narrow and connected to the elastic ligament of the neck and the dorsal portion, which is somewhat shorter and thicker, becoming attached to the spinous

Fig. 349.

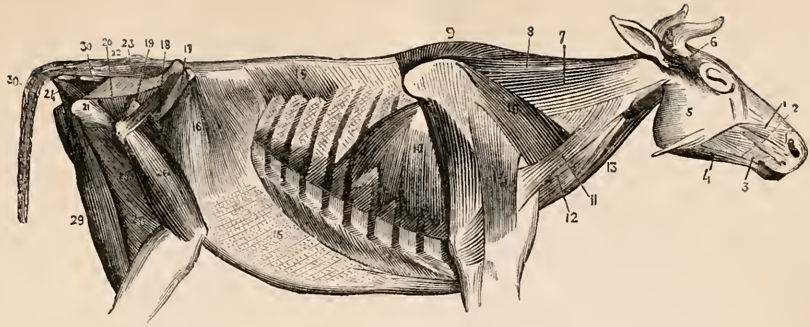


View of the superficial muscles of the trunk in the Ox. (From Gurlt.)

1, orbicularis oris; 2, levator labii superioris; 3, zygomaticus; 4, depressor palp. inferioris; 4 *, risorius santorini; 5, orbic. palpebrarum; 5 *, masseter; 6, corrugator superciliorum; 7, depressor auriculæ; 8, 8, 8, deltoides; 9, sterno-maxillaris; 10, 11, trapezius; 12, latissimus dorsi; 13, pectoralis major; 14, obliquus externus; 15, glutæus maximus; 16, tensor fasciæ latæ; 17, 18, biceps femoris.

* Mercer, On the Structure and Uses of the *Panniculus carnosus*, Med. Gazette, 1840—41, p. 346.

Fig. 350.



View o the deep muscles of the trunk in the Ox. (From Gurlt.)

levat. lab. super.; 2, pyramidalis nasi; 3, buccinator; 4, depressor lab. infer.; 5, masseter; 6, temporalis; 7, splenius capitis; 8, levat. ang. scap.; 9, rhomboideus; 10, serratus major; 11, caput secundum deltoidei; 12, scalenus anterior; 13, caput secund. sterno-maxillaris; 14, abductor brachii superior; 15, serrat. post. inferior; 16, obliquus internus; 17, iliacus internus; 18, gluteus medius; 19, glut. minimus; 20, glut. maximus; 21, pyriformis; 22, levat. caudæ brevis; 23, lev. caud. longus; 24, coccygeus; 25, rectus femoris; 26, vastus externus; 27, adductor magnus; 28, semitendinosus; 29, adduct. tibiæ longus; 30, intertransversales caudæ.

processes of the anterior six or eight dorsal vertebræ. In the Camel it originates from the posterior half of the cervical ligament and the spinous apophyses proper to the first half of the thorax. It is more limited in the Giraffe, where, according to the investigations of Prof. Owen, "it consists of two pretty distinct portions; one arises from the transverse processes of the fifth and sixth cervical vertebræ; its fleshy part is thick and strong, but expands as it passes downwards and backwards, and finally is lost in a strong fascia overspreading the large shoulder joint. The second portion is thin and broad; it arises from the ligamentum nuchæ, and is inserted into the fascia covering the scapula."*

That part corresponding to the clavicular or anterior division of the trapezius in the human subject is widely separated from the muscle just described, and is associated with the *cleido-mastoideus* and *deltoides* so as to form a tripartite mass, for which Cuvier proposed the name of *masto-humeralis*. It is the *levator humeri proprius* of Stubbs, the *communis capitis, pectoris et brachii* of some, and the *deltoides* of others (8,8,8, *fig*.349). In the Sheep and in the Ox it consists principally of two portions with an intervening smaller muscular bundle situated at the centre of the neck, and connecting the clavicular portion of the trapezius to the tendon of the cleido-mastoidens. The superior or more superficial belly becomes implanted into the humerus, while the inferior or deeper division is inserted into the sternum. At their upper attachments the duplicity is very apparent, the broad muscular part being united to the ligamentum nuchæ, and the rounded tendon being fixed to the mastoid apophysis.

After removing the trapezius, our attention is at once directed to a large broad muscle, which in the human subject is represented by the *splenius capitis* and *splen. cervicis*. In the Ox and most other ruminants, the cranial division is alone present; but in the Sheep, according to the researches of Meckel, there are two portions — an anterior or cranial, which is narrow and insignificant, and a posterior of large size, taking its origin by two bundles from the third and fourth cervical vertebræ, to be attached to the transverse process of the atlas. In the Camels both may be said to be absent, but there is a small muscular slip, proceeding from the tendon of the *digastricus* to be inserted into the occiput, which Meckel thinks may constitute a rudimentary form of the splenius capitis.

Beneath the splenius, and often incorporated with it, lies the *trachelo-mastoideus*, which is feebly developed in ruminants and solipeds, but is of large size in the marsupials and edentate mammals. The great *complexus* and *digastricus colli* muscles are united into a single mass, as in the Horse, and in these animals this compound muscle arises by nine or ten fleshy and tendinous slips — intersected by aponeurotic prolongations — from the third cervical to the second or third dorsal vertebræ inclusive. In the Camel there are only seven bundles of origin, and a single long aponeurotic septum, and in the Sheep all traces of the latter are absent.

The *transversalis cervicis* is closely adherent to the trachelo-mastoideus. Separated from the former, there is in some ruminants a muscle, which — corresponding with that portion of the sacro-lumbalis in man, called the cervicalis descendens—stretches from between the transverse apophyses of several of the lower cervical vertebræ to the oblique and transverse processes of certain of the dorsal segments. Meckel alludes to this peculiarity in the Horse.

The *scaleni* muscles, three in number on either side, are very long and powerfully developed in the Camel and Giraffe, presenting in the latter, according to Prof. Owen, four distinct masses, which take their origin "from

* Memoir, *l. c.*

the fourth, fifth, sixth, and seventh cervical vertebræ, and are inserted into the manubrium sterni and first rib." In the Sheep the fleshy bundles are very small; they also arise from the lowermost four cervical vertebræ; but in the Camel they are connected to all the bones of the neck, except the dentata, the posterior scalenus being particularly short, and only attached to the last.

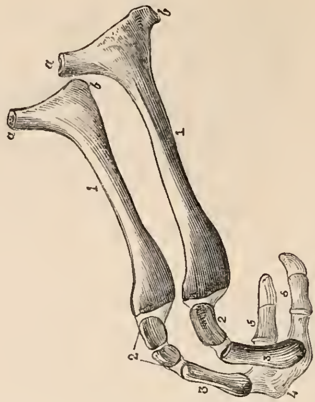
The *longus colli* and *recti* have a similar disposition to those of Man. The former is divided into a superficial and deep portion, the latter division extending as far back as the third vertebræ of the thorax. In the Camel this muscle exhibits an increase of development proportionate with the elongated neck, its posterior attachment commencing at the body of the fourth dorsal segment. The *rectus capitis anticus*, *major* and *minor*, are comparatively insignificant in all ruminants and solipeds.

The muscular arrangements at the fore-part of the neck present many points of interest; for example, — the sterno-cleido-mastoideus of anthropotomists is represented in the majority of mammifers by two distinct muscles. The first of these, the *sterno-mastoideus* or *maxillaris*, is a slender fleshy band which divides near the middle and fore-part of the neck into two portions, one being inserted a little in front of the angle of the lower jaw, and the other becoming attached to the mastoid process. In the Sheep the anterior tendon extends as far forward as the zygomatic arch, and immediately behind the jaw the muscle is united to the deltoides, beneath which it is also connected to the *rectus capitis anticus major* by an intervening tendon. In the Camels this muscle is fleshy throughout its entire extent, and at the lower part is joined to its fellow of the opposite side; superiorly, its tendons are fixed — one to the mastoid process, and another to the maxilla over the region of the submaxillary gland. The characters and position of this muscle are precisely similar in the Giraffe. The situation of the cleido-mastoideus has been already indicated in the description of the tripartite deltoides.

Hyoid apparatus. — Before noticing the muscles connected with the os hyoides it is necessary to direct attention to its osseous framework.

The hyoid bone is made up of a congeries of ossicles more or less consolidated, having relation to totally different parts of the skeleton, but here associated together for the threefold purpose of supporting the tongue and larynx, and affording a *point d'appui* for the muscles destined to act upon these organs. In the ruminant, as in Solipeda, nine distinct elements may be recognised, arranged in four pairs, the ninth piece being represented by the body or *basi-hyal* bone. Fig. 351. indicates the relation of these parts in the sheep. Commencing from above, the first pair—the styloid bones — or *stylo-hyals* (1, 1) are seen to have an enormous longitudinal development, being also somewhat hammer-shaped and compressed laterally, to favour muscular attachment. Their peculiar figure is due to the

Fig. 351.



Hyoid bones of the Sheep. (From Lond. Coll. Surg. Museum.)

presence of two apophyses at the temporal extremity (*a a*, *b b*) and it is by the superior process that the bony chain is connected with the cranium. In the Horse these bones are proportionally longer, but they are shorter in the Camelidæ than in the typical ruminants. In Man the styloid processes of the temporal are homologous with the stylo-hyals. The second pair or *epi-hyals* (2, 2) are intercalated between the first and third series of ossicles, and complete a right angle, formed by the relatively horizontal and vertical position of those bones; they have an insignificant appearance in most of the genera, but attain in the Camels a considerable size. More than two nodules are sometimes present. The epi-hyals are most conspicuous in the carnivorous mammifers, but in the human subject are merely represented by two long ligamentous bands, which in a few instances have been found ossified. The third pair or *cerato-hyals* (3, 3) have a nearly vertical position when the head is raised, and they constitute with the epi-hyals, the lesser cornua which in Man are feebly indicated, being recognised only by two small pisiform nodules moveably articulated to the body of the hyoid, and forming, as in the present instance, a right angle with the greater cornua. In the typical ruminants these elements are larger than the *epi-hyals*, but in the Dromedary, according to Duvernoy, this character is reversed. The body of the hyoid or *basi-hyal* (4), of a triangular form, is placed below the cerato-hyals and anterior to the greater cornua, the four ossicles of which they together consist, being articulated to the extremities of its lateral apophyses on either side. There is generally a slight bulging at the anterior and middle part, indicative of the tendency to antero-posterior elongation, which feature becomes very manifest in other vertebrata, and more particularly in birds; it is to this point that an additional element — the true lingual bone or *glosso-hyal* — is connected, in many of the avian and piscine families, traces of it also appearing in Solipeda and other quadrupeds; it is remarkably large in the Bear. In Camelidæ the basi-hyal presents no anterior protuberance. The fourth pair or *thyro-hyals* — hypo-branchials of fishes and amphibia—(5, 5) represent the greater cornua of the anthropotomist, but in certain mammifers, as in the family under consideration, their extent of development is subordinate to that of the lesser horns. In birds, on the other hand, the length of the thyro-hyals is extreme, the lesser cornua being either rudimentary, or altogether absent.*

The muscles proper to the hyoid chain of bones present many interesting modifications. The *sterno-hyoids* and *sterno-thyroids* (which in Man and mammifera generally, remain distinct throughout their entire extent), are united below in the majority of ruminants, their common band of origin dividing near the middle of the neck, the larger division being connected to the hyoid bone. Meckel states that the sterno-hyoid is entirely absent in the Camel, and Duvernoy remarks the same peculiarity in the Sheep; but Gurlt figures the upper part of it in the latter animal and in the Ox. A muscle analogous to the *omo-hyoid* presents a remarkable difference of origin, relatively, in the typical ruminants, the Camel and the Giraffe. In the Sheep it originates, according to Meckel, in the form of a muscular band of considerable dimensions, which is given off by the rectus capitis anticus major, and leaves that muscle at a point corresponding to the third cervical vertebra to be inserted into the hyoid immediately behind the attachment of the thyro-hyoid muscle. Its relation in the Giraffe will be reverted to presently. In the Camel the disposition of this structure is extremely complicated. From the researches of Meckel we learn that it arises from the anterior division of the transverse process of the fourth cervical vertebra, and is confounded near its commencement with the lowermost bundle of the straight anterior muscle of the head; it subsequently divides into three portions, the first becoming inserted into the lower lip, the second going to the posterior cornua of the hyoid, and the third attaching itself to the lower jaw, upon which it acts as a powerful depressor. Professor Goodsir has remarked to us that an anomaly analogous to this latter distribution is sometimes seen in the human subject. The *stylo-hyoid*, which is absent in certain Carnivora, its place being supplied by a narrow muscle termed the *ceratoido-lateralis*, is present in the Ruminantia, where the latter muscle appears as a prolongation of the stylo-hyoid rather than as a distinct muscle. The first of these two muscles — regarding them as such — proceeds by a long tendon from the posterior and inferior apophysis of the styloid bone, to be attached below to the base of the thyroid cornua; the *ceratoido-lateralis* also descends obliquely from the lesser horn to the greater. In both the above-named families and in the Pachydermata there is likewise a special muscle termed the *masto-styloid;* it is short and triangular, and, arising from the mastoid process of the temporal bone, becomes inserted into the inferior apophysis of the hammer-shaped extremity of the stylo-hyal element or styloid bone, immediately above the origin of the tendon of the stylo-hyoid muscle. The *mylo-hyoid* is distinctly double, the anterior bundle having an extended longitudinal development, while the posterior division is short, and has its fibres directed transversely outward. The *genio-hyoids* of either side are incorporated at the middle line.

In the foregoing description of the muscles connected with the hyoid apparatus we have intentionally omitted those of the Giraffe, preferring, on account of the peculiar interest which the muscular arrangements of this animal present, to treat of them separately. We quote at length, therefore, from the accurate researches of Professor Owen.* "The *mylo-hyoideus* is a thick and strong muscle, it arises from the whole of the internal surface of the lower jaw, and is inserted principally into the *raphe*, or longitudinal commissure, dividing it from its fellow of the opposite side. It adheres firmly to the *genio-hyoideus:* this arises by a well marked tendon from the posterior rugous surface of the symphysis menti, and has the usual insertion. The *genio-glossus* arises by a tendon close to the inner side of the tendon of the *genio-hyoideus;* its fleshy belly has a considerable antero-posterior extent, and diminishes to a very thin edge at its anterior margin. The digastricus has the usual origin, and is inserted, broad and thick, into the under side of the lower jaw. The *stylo-hyoid* is external to the *digastricus*, and is remarkable for the slenderness and length of its carneous part. The most interesting modifications in the muscles of the *os hyoides* were found in those which retract that bone. The muscle which, as in some other ruminants, combines the offices of the *sterno-thyroideus* and *sterno-hyoideus*, arises in the Giraffe by a single long and slender carneous portion from the anterior extremity of the *sternum;* this single fleshy origin is nine inches long, and terminates in a single round tendon, which is six inches long; the tendon then divides into two, and each division soon becomes fleshy, and so continues for about sixteen inches; then each division again becomes tendinous for the extent of two inches, and ultimately carneous again, when it is inserted into the side of the thyroid cartilage, and is thence continued in the form of a *fascia* into the *os hyoides*. We have in this alternation of a contractile with a non-contractile tissue a striking example of the use of tendon in limiting the length of the carneous or contractile part of a muscle to the extent of motion required to be produced in the part to which the muscle is attached. Had the sterno-thyroideus been continued fleshy as usual from its origin through the

* See art. Tongue.

* Memoir, *l. c.* p. 232.

whole length of the neck to its insertion, it is obvious that a great proportion of the muscular fibres would have been useless; for as these have the power of shortening themselves by their contractility only one-third of their own length, if they had been continued from end to end in the *sterno-thyroidei*, they would have been able to draw the *larynx* and *os hyoides* one-third of the way down the neck; such displacement, however, is neither required nor indeed compatible with the mechanical connections of the parts; but, by the intervention of long and slender tendons, the quantity of the contractile fibre is duly apportioned to the extent of motion required for the *larynx* and *os hyoides*. The muscle analogous to the *omo-hyoideus* of other animals, is adjusted to its office by a different and more simple modification; instead of having a remote origin from the shoulder-blade, its fixed point of attachment is brought forward to the nearest bone (the third cervical *vertebra*) from which it could act upon the *os hyoides* with due power and extent of contraction. Its insertion is by a small round tendon."

The muscles of the back and tail present few deviations worthy of remark. The *spinalis* and *longissimus dorsi* exhibit the same attachments as in Solipeda. The *sacro-lumbalis* is proportionately strong in ruminants. The *semispinalis colli*, according to the observations of Meckel, is very largely developed in the Camel, originating from the spinous apophyses as well as from the transverse processes of the five or six anterior dorsal vertebræ. These additional points of origin, while they afford a greater leverage power, constitute at the same time an important peculiarity in this long-necked animal.

The *diaphragm*, which is present in all mammifera, exhibits three openings for the passage of the aorta, œsophagus, and inferior vena cava. A very remarkable feature exists in connection with this muscle in the Camelidæ. It consists in the presence of a small bone situated near the margin of the central tendon. Meckel states that Dr. Jœger was the first to direct attention to this anomaly in the Dromedary and in the Vicugna*, the observation being subsequently confirmed by Dr. Leuckart and himself. In the two-humped or Bactrian Camel its presence was overlooked by the original discoverer, but afterwards ascertained by Meckel to occur in this species also. The bone offers slight variations according to the age of the individual; it is thin and rather more than two inches long in the adult Camel; in the Vicugna it is but feebly developed. Its solidity is not acquired until a late period, for, in a Dromedary about two years old, the cartilaginous matrix only was discernible. In conclusion it may be said that this osseous formation is apparently designed to give support to the diaphragm, which is of great bulk in these animals.

* Syst. der vergleich. Anat. (Fr. edit., tom. vi. p. 212.)

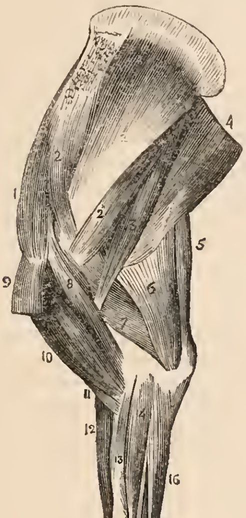
Muscles of the shoulder and fore-limb.—The *trapezius* has already been considered. The *levator anguli scapulæ* (8, *fig.* 350.) varies little from the ordinary mammiferous type. The *rhomboideus* (9) is usually represented by two muscles, *r. minor* and *r. major;* the former, sometimes called the *superior*, arises in the Sheep from the ligamentum nuchæ as far forward as the second vertebra of the neck, and the latter, or *rhomboideus inferior*, proceeds from the spines of the first two or three dorsal vertebræ, the fibres of both converging to be inserted into the upper border of the scapula. In the Horse the muscle is single, and extends forward to the occiput, but is only connected superiorly to the cervical ligament. It is very feebly developed in the Camel, passing only from the spines of the two anterior dorsal vertebræ to the posterior angle of the scapula. In certain Pachydermata and in the Cetacea its appearance is still more insignificant, but it is particularly large in the carnivorous mammals and in the Ornithorhynchus. In the Giraffe it is inserted, like the largely developed serratus major, into the cartilage surrounding the base of the scapula; and in reference to the use of this structure Prof. Owen observes that "as the fore-part of the trunk is, as it were, slung upon the two great *serrati* muscles which principally support the weight of the remarkably deep chest of the Giraffe, the interposition of the elastic cartilages between the upper attachments of the muscles and the capitals of the bony columns of the two fore-legs, must be attended with the same advantage as is obtained by slinging the body of a coach upon elastic springs." * The *serratus magnus* or *major* (10, 10) is exceedingly strong in this order. In quadrupeds generally, it differs from the human subject in presenting a cervical attachment in addition to its costal connection. In the Sheep it has no less than thirteen bundles of origin, eight of which come off from a corresponding number of the superior ribs, the remaining five proceeding from the transverse apophyses of the third to the last cervical vertebra inclusive. In other ruminants there is a slight numerical variation in regard to the fleshy digitations, but their general disposition is the same, being in all cases subsequently united and implanted into the base of the scapula, there forming, in conjunction with the trapezius, a sling-like support to the anterior extremity. The *serratus minor* has an arrangement in mammifera similar to that of its anologue, the lesser pectoral of the human subject; but in the latter it is inserted into the coracoid apophysis of the scapula, while in the former it is usually connected to the humerus. In many carnivorous, edentate, and marsupial families this muscle is entirely wanting.

The *latissimus dorsi* (12, *fig.* 349.) is somewhat feebly developed in ruminants, but its attachments are similar to those in Man. The *pectoralis major* (13, *fig.* 349) is proportionately

* Memoir, *l. c.*

greater, and divided into two,—a small fleshy bundle proceeding from the anterior extremity of the sternum to the lower part of the humerus, and a larger mass coming off from the whole length of the sternum posterior to the former, its fibres passing obliquely forward to be inserted into the external tuberosity of the same bone. There is an additional muscular slip in the Sheep and Horse, by the action of which the crossing of the fore-legs is produced; this is denominated by hippotomists the *ambibrachialis communis*. Cuvier remarks the same muscle in Cetacea. Corresponding to the scapular division of the deltoid in the human subject, there is, in ruminants and solipeds, a muscle called the *abductor longus brachii* or *abd. brach. superior* (14, *fig.* 350.); it generally exhibits two points of

Fig. 352.



Superficial layer of muscles of the fore limb of the Ox. (From Gurlt.)

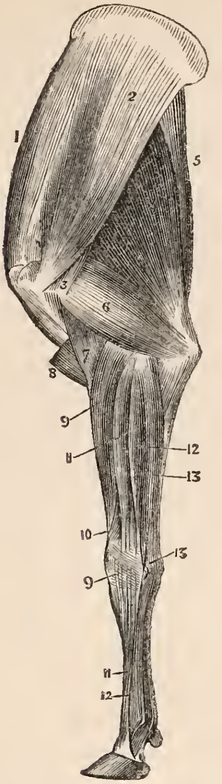
1. supra-spinatus; 2, infra-spinatus; 3, abductor brevis; 4, anconeus longus; 5, exten. cubiti longus; 6, ancon. externus; 7, brachialis internus; 8, deltoides; 9, 9, exten. carpi radialis; 10, abductor pollicis; 11, 11, extensor digit. longior; 12, 12, exten. digit. brevior; 13, 13, flexor carpi ulnaris externus.

attachment above, one at the spine of the scapula, and the other from the infra-spinous fossa. On their passage down, the fibres coalesce, and become inserted by a common tendon into the linea aspera of the humerus. The external scapular muscles, viz., the *supra-spinatus* (1, *fig.* 352.) and *infra-spinatus* (2), are powerfully marked in this order; the former is implanted by a double tendon of insertion into the anterior and internal tuberosities of the humerus, the latter being connected below to the external tuberosity. The round muscles have the same attachments as in man, but the *teres major* or *t. externus* (3, *fig.* 353.) is in Ruminantia and Solipeda smaller than the *teres minor* or *t. internus* (2, *fig.* 353). The *sub-scapularis* (2, 2 *fig.* 353.) is of large size, and subdivided.

The *coraco-brachialis* (8, *fig.* 353.) is always present, although there be no indication of a coracoid apophysis; the greater part of the muscle lies deep, and is connected to the inner border of the upper half of the humerus, the remainder lying more superficially, and continuing as far as the internal condyle into which it is implanted. The *biceps brachii coraco-radialis* or *flexor cubiti longus* (10, *fig.* 353.) has a similar disposition to its analogue in Man; but in Carnivora and Solipeda, where the coracoid process is absent, it exhibits but one head. In the Bear, according to Cuvier, the absent division is represented by a muscular slip passing off from the coraco-brachialis. Meckel states that in the Camel and Dromedary the apparently single tendon of origin arises from the margin of the glenoid cavity as usual, but it is very thick, and can easily be separated into two portions, which are united only by cellular tissue. These, as they pass over the head of the humerus, swell out and enclose between them a sesamoid body consisting of fibro-cartilage; the external of the tendons is the larger, and also subdivides, giving off a strong tendinous cord which becomes incorporated with the antibrachial aponeurosis. The *brachialis internus*, or *flexor cubiti longus* (7, *fig.* 352. and 11, *fig.* 353.), is comparatively weak. In the typical ruminant it rises from the posterior and external part of the neck of the humerus, but in the Camel it commences lower down from the middle third of the bone, its tendon of insertion in all cases being anterior to that of the long flexor. The divisions of the *triceps extensor cubiti* are described under different names by hippotomists, but this disposition is similar to that of Man. The *extensor cubiti longus* (5, *fig.* 353.) is the *extensor magnus* of Bourgelat; the *extensor brevis* is the *extensor medius* of the same author, and the *anconeous longus* of Gurlt; the *brachialis externus* is the *extensor brevis* of the former and the *anconeus externus* of the latter. There is also another muscle termed by Gurlt the *anconeus internus* (7, *fig.* 353.).

The Ruminantia and Solipeda are generally described as possessing neither *supinators* nor *pronators*, but the above-named author figures in the Ox a small muscular bundle, which he calls the *pronator teres* (13, *fig.* 353.); and moreover Meckel points out the rudiments of this muscle in the Camel, remarking at the same time that its function is no longer that of a pronator but of a flexor. The *extensor carpi radialis* (9, *fig.* 352.) is single in the Camelidæ, as in the Horse, rising from the external condyle and inferior fourth of the hu-

Fig. 353.



Deep layer of muscles of the fore-limb of the Ox, viewed from within. (From Gurlt.)

1, supra-spinatus; 2, 2, subscapularis; 2*, teres minor; 3, teres major; 4, latissimus dorsi; 5, extensor cub. longus; 6, anconeus longus; 7, ancon. internus; 8, coraco-brachialis; 9, pectoralis major; 10, biceps brachii; 11, brachialis internus; 12, extens. carpi radialis; 13, pronator teres; 14, flexor carpi radialis; 15, flexor digit. sublimis; 16, flex. carpi ulnaris internus.

merus to be inserted into the base of the cannon bone at the fore-part. Antagonistic to this, is the *flexor carpi radialis* (14, *fig.* 352.), the tendon of which is connected to the base of the cannon bone behind. The tendons of the *extensores digitorum longior* (11) and *brevior* (12, *fig.* 352.) separate in front of the foot, the divisions of the former being inserted into the base of the ultimate bones of the toes, and those of the latter into the distal extremities of the penultimate phalanges. A muscle corresponding to the *abductor pollicis* (10) is present, notwithstanding the absence of the thumb, and becomes attached to the inner aspect of the inferior end of the cannon bone. The *flexores carpi ulnaris externus* (13) and *internus* (16, *fig.* 352.) are both inserted into the pisiform bone. The tendons of the *flexor digitorum sublimis* (15, *fig.* 352.) and of the *flex. digit. profundus perforans* remain distinct, the latter piercing the former as usual, to be implanted into the base of the distal phalanges of either toe.

Muscles of the haunch and hind-limb.—The *gluteus maximus* (15, *fig.* 349.), which is but feebly manifested in all quadrupeds, owing to the horizontal position of the body, has an insignificant development in ruminants. It rises from the crest of the ilium and sacral fascia, receiving in its passage down a strong tendon from the *tensor fasciæ latæ* (16, *fig.* 349.); the tendon proper to the glutæus becomes inserted below the trochanter, while that of the tensor is continued on in front of the tibia, performing in some measure the office of a flexor. The *biceps femoris* or *vastus longus* of Bourgelat (17, 18, *fig.* 349.), is a muscle of striking proportions in this order and in solipeds. It originates by two distinct heads, one of which proceeds from the tail and sacro-sciatic fascia, and the other comes off from the tuberosity of the ischium; the fibres of both proceed downward, and are inserted, the former chiefly into the head of the tibia, and the latter into the general aponeurotic covering of the leg. In consequence of the posterior border of the front division overlapping the ischiatic portion, there results a well marked groove or raphé, forming a characteristic feature externally on the skin as when the muscle is in action; this is better seen in the Horse. The arrangements of the *iliacus internus* (17, *fig.* 350.), *glutæus medius* (18), and *minimus* (19), and *pyriformis*, are similar to those in Man, differing mainly in proportion, the last named being particularly small; the same observation applies more or less to the *obturator externus* and *internus*, the *gemelli*, *quadratus femoris*, *vasti* and *adductores*, the two groups of muscles comprehended under the latter titles being chiefly interesting on account of their great size and strength.

Having already extended our myological descriptions beyond the prescribed limits, we conclude this part of our subject by observing that the muscles of the hind leg resemble those of Solipeda so closely as scarcely to demand a separate notice, while those acting upon the digits have the same general disposition as in the fore limb.

Integumentary System. — Under this head we proceed to indicate very briefly certain peculiarities of the hair, and more particularly the elastic cushion of the sole of the foot, and the remarkable protuberances situated on the back of the Camel.

While the growth and condition of the cuticular layer of the skin in the different classes of ruminants is of the highest importance in an economic point of view, it is not the less certain that the phases of development through which the integumentary covering passes — its varied aspect and periodicity of renewal, together with the causes which induce such changes — are matters of high interest to the physiologist.

In no group of mammiferous quadrupeds have we a more striking example of the adaptation of structure to the exigences of the creature than obtains in the remarkable dorsal ump, and in the cushion-like sole-pad of the Dromedary.

The hump consists essentially of adipose matter, developed in the subcutaneous areolar substance, its secreting cells having undergone an extraordinary local increase. To support such a mass, the connecting tissue exhibits a corresponding augmentation, the fibres assuming the character of ligamentous bands, which are firmly united below to the capitals of the bony columns of the dorsal vertebræ. In reference to the function of this growth travellers have ascertained beyond all controversy that it serves as a store-house of nourishment, affording to the animal, in conjunction with the stomachal water-cells, a provision against the inanition which long journeys would otherwise entail. In accord with this statement, it has been observed that the hump of the Dromedary becomes attenuated and reduced under circumstances of impoverishment, while, on the contrary, it is marked by rapid increase and ultimate plumpness when the supply of food is abundant.

The general character of the dermal envelope in Camelidæ deserves little comment; the hair is coarse and shaggy in the typical species, and of a soft woolly texture in the Auchenias, where it is also very long. At certain points it acquires in the Camel a rigid bristle-like character, this being especially manifest at the under part of the feet, near the margin. In this spot, however, the hairs are scanty, and they are entirely absent for a small space, over the so-called knees, and at the under and fore-part of the chest, where from constant pressure during the recumbent posture of the body, the cuticle acquires a horny consistency. These callosities are not present in the Llama.

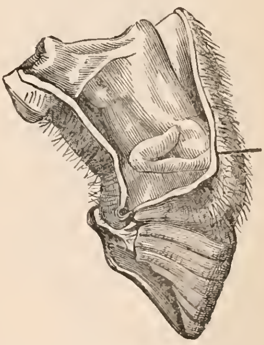
One of the most interesting anatomical features, forming a distinction between the two cameline genera, consists in the degree of organisation of the foot-pad and corneous investment of the toes. In the Camels, properly so called, the digits are more or less completely imbedded in the broad elastic cushion which extends for a considerable distance laterally on either side of the foot, binding and fixing the phalanges immoveably together; while at the same time it is particularly worthy of remark, that the hoofs are merely represented by two rudimentary nails situated on the dorsal surface of the tip of each toe. In the Llamas the sole-pad is double and narrow, each division being limited to one side of the cloven foot, while the nails, instead of being weak, are very powerfully developed, and strongly curved. In consequence, therefore, of the easy separation of the toes, combined with the modifications of the pad and hoof here referred to, it is at once evident that such a condition of the foot is peculiarly adapted to an animal whose life is destined to be spent, unlike that of his more highly valued congener, on the rugged slopes and precipices of a mountainous district.

In the solid-horned Ruminantia very important changes coexist with the shedding of the antlers. These organs occupied our attention when describing the anatomical relations and development of the horns; but, as some physiologists are disposed to regard them as part of the dermo-skeleton, we take this opportunity of reverting to the subject. If such a view as the one here mentioned be not supported by the mode of growth, it acquires nevertheless an appearance of consistency when we bear in mind that the annual shedding of the horns takes place contemporaneously with that of the hair. By others, this simultaneous loss of structure is regarded as a mere coincidence, affording no proof, they say, of the integumentary character of the cranial outgrowths, but rather indicating a special provision, for the explanation of which we are to look to another source. This argument is followed up by assuming that, were it not for the change alluded to, the young Deer would sustain injury from the *bucks*, which, at the period of the full evolution of the antlers, exhibit a destructive and relentless ferocity. After the loss of the offensive weapons, it is well known that their disposition acquires a milder habit. In furtherance of this view of the question we are likewise reminded that it is necessary to associate the persistency of the horns of the Giraffe with the equally well ascertained fact, that in this aberrant cervine genus, there is, as in Cervidæ proper, a periodical desquammation of the cuticle not affecting the hairy covering of the cranial epiphyses, and involving no subsequent alteration in the animal's psychical character, which, under ordinary influences, is proverbially gentle, and always the same.

In a former part of this article, reference has been made to the epidermic nature of the corneous investment of the bony cores in *cavicornua*, and the extension of it found prolonged over the frontal region in the Buffaloes, a tribe exhibiting an approach to the Pachydermata in many respects, and more especially in the organisation of the hide, which has a leathery consistence, and is scantily provided with stiff bristly hair.

In conclusion we may remark that the cloven condition of the hoof in the typical ruminant is evidently designed to impart lightness and elasticity to the spring; and, in order

Fig. 354.



Foot of the Sheep.

to give full effect to such an arrangement, many species are provided with a special glandular sebaceous follicle between the toes, whose office is to furnish a lubricating secretion, calculated to prevent injury from friction of the digits one against the other. *Fig.* 354. represents the position and dimensions of this organ in the Sheep. According to Sir Charles Bell there is yet another intention in this cloven form, viz., that of aiding the voluntary elevation of the foot when it has sunk deeply into soft ground. "We may observe," he says, "how much more easily the Cow withdraws her foot from the yielding margin of a river, than the Horse. The round and concave form of the Horse's foot is attended with a vacuum or suction as it is withdrawn; while the split and conical shaped hoof expands in sinking, and is easily extricated."*

Digestive System. — *Buccal Cavity.* — The lining mucous membrane of the oral cavity is very rough, being covered throughout with very prominent papillæ. At the roof of the mouth they have a flattened form, and are arranged in parallel rows, producing a series of ridges or bars, the margins of which are denticulated and directed backward. They are very conspicuous in the Camel, and in the Giraffe we have counted from fourteen to eighteen rows; the papillæ of the anterior ridges, however, lose much of their linear arrangement. Respecting the use of this peculiar grooved structure, Mr. John Zaglas appears to have offered a satisfactory solu- ion. Speaking of the action of the tongue during deglutition, he says, "I may here hazard the opinion, that the transverse rugæ on the palate of Man and the lower animals are intended, to a certain extent, for the support of the tongue in the act of elongating itself backwards. The varieties which they exhibit coincide with what would appear to be required in the relations of the tongue and oral cavity. In Man, in whom the alveolar process is perpendicular, they are slightly developed, and situated far forward. In the lower animals, in which the alveolar process is small or oblique, the rugæ are situated farther back, and are more fully marked, particularly in those which swallow bulky and comparatively rough morsels, as in the ruminants and solipeds."† The oral roof of the Giraffe is marked by an extensive deposit of leaden-coloured pigment, stretching from the alveolar margin to the centre of the palate; small isolated patches also occurring still farther back. A callous thickening of the gum occupies the place and supersedes the function of the non-developed intermaxillary incisives. The buccal papillæ attain their greatest size in the region of the cheek opposite the true molars. In this position they take on the character of horny spines, very like those seen in the œsophagus of the Turtle. They have either the form of simple elongated cones, or are aggregated together, and blended so as to present two, three, or even four points. This complicated disposition is well shown in the accompanying figure (*fig.* 355.) from the Camel; in

Fig. 355.

Buccal papillæ of the Bactrian Camel. (From F. Müller and Wedl.)

the Giraffe the longest spines, which are fully half an inch in length, give off secondary processes, thus resembling very closely the fungiform papillæ of the human tongue after the epithelial layer has been removed. Professor Owen is of opinion that the principal function of these organs consists in adjusting the bolus during mastication.

Teeth. — Consistent with the compound character of the ruminant stomach, a parallel complexity obtains in the structure of the teeth, at least, in those concerned in triturating the food.

In those families which have *incisives* in the lower jaw only, *these* exhibit simple trenchant crowns, which slant horizontally forward; and being opposed only by the hardened gum of the upper jaw, the function they perform during the act of feeding is rather that of breaking or tearing, than cutting. The action is accompanied by a swinging movement of the head forward, the powerful muscles inserted into the occiput along with the elastic ligamentum nuchæ, rendering such a motion almost effortless. In Œgosceridæ, Bovidæ, and Cervidæ generally, where the incisors form a broad line at the expanded tip of the lower jaw, the extent of their grasp is considerably increased by the prominent position of the *canines* on either side. These latter partake of the function ascribed to the former, and their aspect is so similar that many anatomists have been led into error respecting their true nature. In the Giraffe the canines present divided crowns, and are not placed so far in front; nevertheless, they are closely applied to the outer incisors, the whole series together forming a semicircle.

The characters of the *molar* teeth chiefly demand consideration in this place. These, though presenting every variety and modification of contour in the different families, manifest at the same time a certain uniformity of type throughout the entire order. A sin-

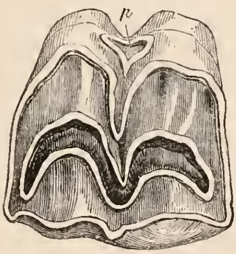
* Bridgewater Treatise, p. 92.

† Goodsir's Annals of Anatomy and Physiology, Part II. p. 122.

gle example will illustrate the points most deserving of attention.

The true molar tooth of the permanent series has a quadrilateral form, its outer and inner lateral surfaces being bounded by margins more or less convoluted. The crown in the young state presents four elevated cusps, which, by subsequent attrition, disappear. The ground surface, thus flattened, is marked in the centre by double crescent-shaped ridges of enamel, so disposed as to present, along with the central mass of *dentine* and external crust of *cementum*, alternate layers of hardened tissue, having different degrees of density. By such an arrangement it consequently follows that the enamel being the least affected by trituration, remains somewhat above the level of the other dental substances,—a condition highly favourable for the due performance of mastication, and one resulting in all cases from the vertical folding of the original formative capsule. The upper molars of certain individuals present an accessory island-shaped portion of enamel at the internal border, by which the extent of grinding surface becomes enlarged. This additional facet only makes its appearance in a tooth which has been employed for some time, as it depends upon the wearing down of a columnar fold which is developed at the side between the lobes, and which does not extend so high up as the summit of the crown in the unworn tooth; it is well seen in the Ox and Deer (*p*, *fig.* 356.)

Fig. 356.



Molar tooth of the Deer.
(From Owen's "Odontography.")

Tongue. — The lingual organ undergoes certain modifications, in accordance with the habits and kind of aliment on which the ruminant subsists. These peculiarities do not involve any material departure from the type of structure invariably found in other mammifers ; on the contrary, the muscular elements and their relations to surrounding parts remain nearly the same. The deviations of which we have to speak principally refer therefore, to the form of the organ and its epidermal covering. In Ruminantia, more than in almost any other order, the tongue is specially designed to fulfil the offices of prehension as well as deglutition, and it necessarily follows that the several portions of the machine destined to carry out such complicated functions, exhibit a corresponding complexity of development. Those regions, arbitrarily denominated by the anthropotomist the *root*, *body*, and *tip*, acquire great significance in this group of animals, being morphologically indicated on the dorsal aspect of the organ ; and they not only manifest a structural distinctiveness, but the functions over which they preside subserve different purposes. The anterior moiety is employed in collecting, and perhaps in some measure ascertaining the nature of the food ; the second aids in adjusting and preparing the morsel, but is more particularly concerned in thrusting the bolus backward into the œsophageal cavity ; while the third circumscribes and regulates the movements of the organ in its entirety, acting from the *point d'appui* of the hyoid bone (Zaglas).

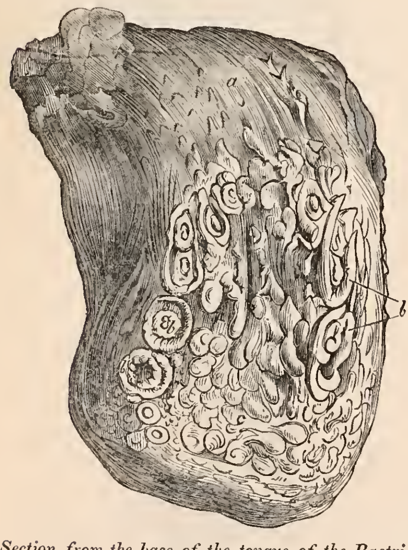
The surface of the tongue is armed with forms of papillæ similar to those of Man and other mammalia. Two kinds, namely, the simple *filiform* and *fungiform*, are conspicuous and very numerous on the dorsal aspect of the elongated prehensile portion in front, and two other varieties — the *conical* and *circumvallate* — occupy the dorsum towards the root, leaving the inter-molar region comparatively free. Of those papillæ at the fore part, the simple filiform are curved back-

Fig. 357.

Tongue of the Giraffe. (From Owen.)

ward, and are by far the most abundant of all these structures; they are very closely set together at the tip, and have a horny epidermal covering, approaching in this respect the rasp-like retroverted spines on the tongue of Carnivora. The *fungiform* or spherical gustatory papillæ are sparsely scattered here and there, but somewhat closely aggregated at the lingual margins. In the Giraffe, notwithstanding the deposition of a dark purple pigment which distinguishes the anterior half of the tongue, the last named papillæ present a very striking appearance, resembling so many small highly polished beads of a deep black colour. They are well shown in the annexed woodcut (*fig.* 357.). The conical papillæ situated behind and towards the root, may be grouped under the same category as the retroverted filiform spines seen in front; but as they proceed in the direction of the pharynx their conoidal character becomes obliterated, and they assume a more or less flattened oval or rounded form. The *papillæ circumvallatæ*, though not occurring in great numbers, are largely developed, and in the Camel exhibit a very complicated structure (Meckel); the middle projecting portion, instead of being smooth and single, is split up, as it were, into numerous finely serrated secondary filaments, leaving a small central depression unoccupied, while the elevated circumferential margin outside the circular fossa shows at the same time a tendency to subdivision (*b*, *b*, *fig.* 358). In the Giraffe

Fig. 358.



Section from the base of the tongue of the Bactrian Camel. (From F. Müller and Wedl.)

and Deer they offer a faint indication of the central dimple, but their character otherwise accords with the appearances usually presented.

The *muscles* of the tongue, as already hinted, display few marked deviations from the ordinary mammiferous type; nevertheless, the comparative glossologist recognises in these slight differences, points fraught with peculiar anatomical and physiological interest. To enunciate this speciality fully in all its bearings would demand more time and space than has been placed at our disposal, and it is not without regret that we are compelled to limit the exposition of so captivating a subject to the few following remarks, gathered in great measure from the monograph of Mr. Zaglas and the observations of Professor Owen on the tongue of the Giraffe. Fortunately, we have had an opportunity of confirming the previously recorded particulars concerning the lingual organisation of this remarkable animal, and in regard to the myological arrangements of the tongue in other ruminants, the writings of Cuvier, Blandin, and others, furnish some important details.*

The *styloglossus* rises from the lowermost extremity of the styloid bone, and extends along the under surface of the tongue as far as the tip, being separated only from the muscle of the opposite side by the interposed *genio-glossi*. It is powerfully developed in the Giraffe, and is confined in its position by strongly marked bands of muscular fibre directed outwards from the superior border of the genio-glossus (where that muscle dips into the medullary substance), to the marginal expansion of the lingual fascia investing the dorsum. This muscle is of small dimensions in the Camel. The *hyo-glossus* is a compound structure, its several portions differing only from those in man by being more distinct and widely separated; the division recognised as the *cerato-glossus* by the human anatomist is usually described as the *stylo-glossus minor* in the lower animals. The *genio-glossus* varies considerably in size, and is unconnected with any part of the hyoid apparatus (Blandin); ordinarily, the laminæ of each muscle are easily parted in consequence of the looseness of the interposed areolar substance as far as the mesial line, where the fibres begin to dovetail into one another. In Man the fasiculi are short and comparatively thick, but in the Deer and Camel the two muscles are thin and united anteriorly. These applied muscular laminæ are very strong, and have a great longitudinal extension in the Giraffe; posteriorly they admit of easy separation, but in front the fibres are intermixed, attenuated, and with difficulty isolated. In connection with this part of the subject it may be remarked that the researches of Mr. Zaglas have shown the septum (*linea albescens* of Caldani) or cartilago-lingualis to have no real existence in the Sheep, Deer, Calf, or Camel; and we may add that our own examinations prove that this structure is likewise absent in the Giraffe. The value of this observation is enhanced when we bear in mind, that in other mammals — the Carnivora more especially — this

* Blandin, Thèse Inaug. sur la Structure de la Langue de Bœuf; also, Mémoire, &c., Archiv. Gén., tom. i. 1823.

septal fibro-cartilaginous aponeurosis (which we take to be the homologue of the true lingual bone), is strongly indicated.

Much confusion has arisen in regard to the muscles constituting the cortex of the tongue. The general term lingualis has been applied to numerous muscular bundles situated on the dorsum immediately beneath the lingual fascia. According to Gerdy they may be arranged in four groups * ; of these the most superficial layer appears to be quite distinct from the rest, and on this account it has been separately described as an independent muscle by Bauer and Zaglas, the latter aptly designating it the *noto-glossus*. This superficial muscular mass spreads over the whole upper surface of the tongue; it apparently exists in all mammifera, being more highly developed in some than in others; it is feebly indicated in the Camel. Without accepting the following inference, we may remark that Dr. Mercer, in his "Anatomical Observations on the analogous Structure of the Lingualis and Panniculus Carnosus," endeavours to show that one of the principal offices of the lingualis is to erect the rasp-like papillæ; and it is evident that he only attributed this function to that portion of the muscle, since denominated the *noto-glossus*, for, he adds, "the first" layer of the lingualis, "which is the most conspicuous, can alone act on the surface of the tongue and its papillæ."† The fibres of the *lingualis*, properly so called, take their origin from the lingual margins near the root, and pass transversely or obliquely inwards to a point a little beyond the middle line; in the short-tongued quadrupeds and in Man the bundles reach as far forward as the tip, but in the ruminants their extension is comparatively limited. Respecting the disposition of the associated muscular filaments, collectively termed the *transversus*, considerable difference obtains in regard to what may be called the fibres of insertion. In the ruminant type, where no lingual septum is present, the fibres decussate with those of the opposite side, extending therefore beyond the mesial plane, while on the other hand, in Man and animals having a well-marked *linea albescens* — such as is seen in Carnivora — the fibres do not pass beyond the middle line, but are intimately united to the septum (Zaglas). The *perpendicularis externus* offers nothing remarkable, and the *glosso-palatinus* and *glosso-pharyngeus* have no existence in this order.

The distribution of the *vessels* and *nerves* of the tongue have the same general arrangement as in other Mammalia; but in consequence of the greater longitudinal development of the organ they exhibit a corresponding augmentation. Prof. Owen remarks a disparity of calibre affecting the lingual arteries of the Giraffe, that of the left side being paramount and anastamosing freely with the vessel of the right side as far as the commencement of the prehensile portion — judging from the lithographed representation appended to that distinguished anatomist's "Memoir." Our own specimen exhibits this peculiarity in a still more striking degree, the left vessel being — as compared with the right — a mere arterial twig. We have not found this vascular anomaly in the Cervidæ proper, neither is it present in other allied genera. The lingual *veins* in Camelopardalis are particularly broad and somewhat plexiform, and the nerves, in the retracted condition of the tongue, are beautifully tortuous.

The *salivary glands* are chiefly noticeable on account of their large dimensions and elongated excretory passages. The orifices of the Whartonian ducts, are visible at the anterior part of the mouth beneath the tongue, and in the Giraffe are protected by two small membranous valvular folds fringed with papillæ. The tonsils are bulky, and in the Camel communicate with the oral cavity by numerous canals, the apertures of which are surrounded by slight prominences of the mucous membrane. In Camelopardalis, the amygdala assume a higher type of structure, and open by a short common duct capable of admitting the tip of the little finger. There is yet another peculiarity in the faucial region of this aberrant cervine genus, arising out of the presence of a rudimentary uvula, which on close inspection we find to be made up of three minute papillæ, intimately conjoined at their bases.

The *œsophagus*, in accordance with its functional activity in this family, is thick and fleshy. It is surrounded by two distinct layers of muscular tissue — an outer and inner: the fibres of the former being transversely circular, those of the latter obliquely longitudinal. They have a deeper colour than obtains in the non-voluntary muscles, but do not exhibit any transverse striæ; in some particulars, however, microscopic investigation has shown them to resemble very closely the voluntary type (Owen).*

The ruminant *stomach* affords a striking illustration of the *special* evolution of a complex mechanism from the *general* or more simple type of structure, and to the mind of the unprejudiced truth-seeker it irresistibly indicates evidence of design; this train of reasoning is not weakened by the fact that two, if not three, of its divisions are essentially dilatations of the lower extremity of the œsophagus.

The first compartment or *Paunch* (*b, fig.* 359.) — otherwise called the *Rumen*, *Ingluvies*, or *Panse* — occupies a considerable proportion of the abdominal cavity. It is the largest of the four stomachs, and its general form is that of a square with rounded angles. Externally there are two well-

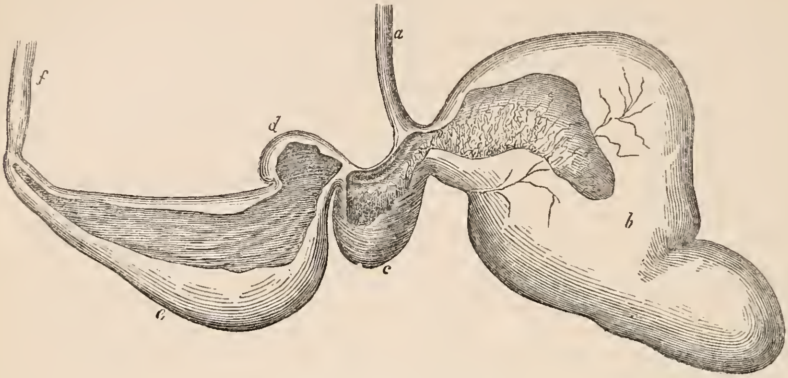
* Gerdy, Anat. et Physiolog. de Langue: Archives Génerales de Médecine, tom. vii. p. 363.

† Anatomical Observations, &c. Edinburgh, 1841.

* The sharks, which possess the power of ejecting their stomachal contents, have the muscular fibres of this viscus marked by transverse striæ. We have seen this in *Lamna cornubica*.

marked constrictions, corresponding to folds of the lining mucous membrane; and thus subdivided, the viscus resembles, as it were, an enormously distended coil of intestine bent into the figure of an italic *S*. In the typical species the internal surface is densely beset

Fig. 359.

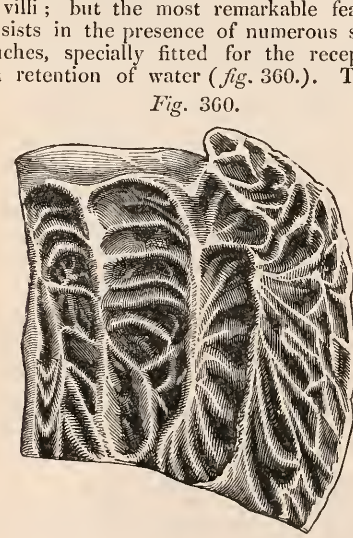


Composite stomach of the Sheep.

with villi; these give to the membrane a peculiarly rough aspect, and at different portions of the cavity their form is curiously modified. Usually they are remarkably prominent, pedunculated, more or less club-shaped and compressed; or they may be tapering and pyriform. In some localities their size is insignificant, and they almost disappear at the margins of the salient folds. In the Giraffe we find their dimensions strikingly uniform at one spot, while, in another region great irregularity in this respect is observable; the same remark holds good in other horned species, where the deviations from this type are too slight to merit a separate notice.

The organisation of the paunch in the Camelidæ differs very materially from that of the ordinary ruminant. Instead of presenting a rough internal surface, crowded with villosities, the mucous membrane is conspicuously smooth and entirely destitute of villi; but the most remarkable feature consists in the presence of numerous small pouches, specially fitted for the reception and retention of water (*fig.* 360.). These

Fig. 360.



Water-cells in the paunch of the Camel.

sacs, which may be looked upon as so many diverticula developed from the walls of the cavity, are arranged in two distinct groups — one on the right side and the other on the left; the former being by far the larger, and in the adult Dromedary measuring about one foot and a half in length, and six inches in breadth (Meckel). The cells of each batch are disposed in parallel rows, separated from one another by strong muscular bundles, given off from a single large band of fibres which commences at the cardiac extremity of the rumen, and proceeds in a longitudinal direction, dividing the entire cavity into two compartments. The muscular fasiculi are arranged transversely, and give off secondary bundles at tolerably regular intervals, so that the rounded orifices of each sacculus are guarded by powerful square-shaped muscular sphincters. Some of the cells are more complicated than others, being subdivided into numerous loculi by folds of the lining membrane. The largest of the reservoirs in the adult Dromedary, when dilated, have a depth and width of about three inches. In the Llamas the structure of this apparatus, though more feebly indicated, is very similar to that of the Camels, properly so called.

The second stomachal viscus (*c*, *fig.* 359),— otherwise called the *reticulum bonnet*, or *water-bag* — has a globular outline, — is of much smaller dimensions than the paunch, and forms a sort of cul-de-sac between it and the third cavity. It originates in common with the rumen, and like that organ may be regarded as a kind of hernial dilatation of the lower end of the œsophagus. By some it has been looked upon as a mere appendage to the former, being continuous with it at the upper and anterior part, and separated only by a projecting membranous fold, precisely similar to those met with in the first cavity. In the typical species it is distinguished internally by the presence of a multitude of acute-angled polygonal cells, and from this circumstance has been vulgarly denominated the *honey-comb-bag*. The cells are particularly shallow in the Rein-deer and Giraffe, being circumscribed by very narrow laminæ, scarcely elevated above the level of the mucous surface. The lining membrane is further characterised in the horned ruminants by a cuticular covering developing a great number of minute and sharply pointed conical papillæ, which occupy every part of the cavity, but are most prominently marked along the ridges of the laminæ, imparting to these folds a denticulated aspect. In the Camels and Llamas the honeycomb-cells acquire a form and capacity strictly analogous to the water-cells of the paunch; but there are some slight modifications of structure, apparently conformable with the more temporary or immediate purposes which they subserve. The apertures of the cells of the rumen — destined to retain water for a lengthened period — are narrow and guarded by productions of the lining membrane, while those of the reticulum, constantly parting with their aqueous contents during the ordinary act of rumination, are more patent, and not covered in by special membranous folds; moreover, in the distended condition of the cells, the external surface of the paunch is marked by a corresponding number of vesicular bulgings, but in the reticulum the walls remain smooth and do not exhibit any very evident traces of the contained water-cells; their internal subdivisions are likewise more numerous and complicated than in the rumen. Another distinction — already alluded to — between the typical and akeratophorous species, obtains in the absence of an internal cuticular epidermis in the bonnet of the Camelidæ. In all ruminants at the anterior border of the second stomach is situated a short demi-canal, constituting the remains of that portion of the œsophagus not involved in the great gastric dilatations, two of which we have now described. This elongated channel — very well shown in the accompanying woodcut, *fig.* 359., — forms a bond of communication between the gullet and the three first digestive cavities, and it is provided with an extension of the muscular tunics of the œsophagus, modified to suit its twofold office, to which we shall again have occasion to refer when speaking of the ruminating function in detail.

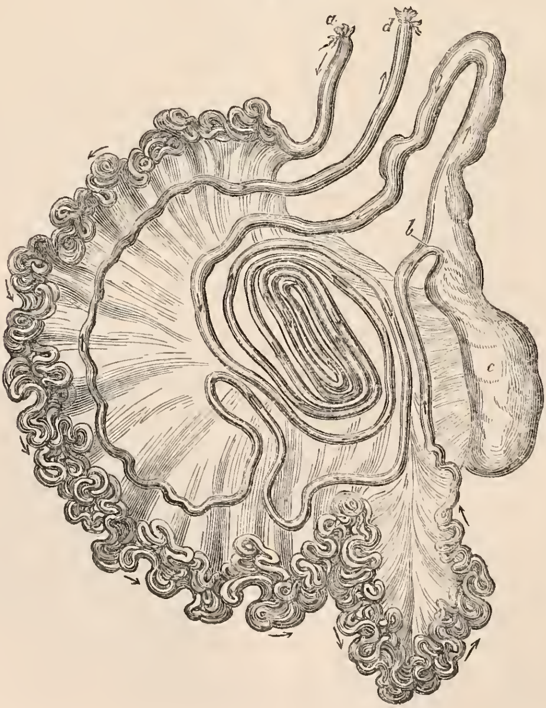
The third stomach (*d*, *fig.* 359.), commonly called the *Psalterium*, *Manyplies*, *Omasus* or *Feuillet*, intervenes between the water-bag and the fourth or true digestive cavity, communicating with the former by a constricted orifice and with the latter by a very wide opening. It is the smallest of the stomachal viscera, subglobular in form, and smooth externally; but the extent of its absorbing surface bears no relation to the diminished bulk of the organ, seeing that it is enormously increased by a remarkable folding of the internal lining membrane, the duplicatures of which resemble the leaves of a book, — hence the names above indicated. The laminæ are longitudinally disposed, and in the empty condition of the viscus are closely applied against each other. In breadth they exhibit proportionate differences, so that we find an alternating assemblage of laminæ presenting three several degrees of development; one, a very narrow fold, another, very broad, and a third of intermediate width, serially intercalated between the two. Altogether about forty such septa have been counted in the Sheep, and more than double that number in the Ox. The internal surface is beset throughout with small conical, pointed papillæ, similar to the villi of the reticulum, those placed at the free margins of the folds being paramount. In Camelidæ the psalterium is greatly elongated, attenuated at either extremity, and three or four times more bulky than the water-bag; otherwise, its organisation conforms with the peculiarities observable in the horned species.

The fourth stomach (*e*, *fig.* 359.), technically termed the *Reed*, *Abomasus*, or *Caillette*, constitutes the true digestive apparatus, analogous to the simple gastric organ of the non-ruminating vertebrata. It is about one third of the size of the paunch, and smooth externally, has an elongated pyramidal figure, and terminates by a narrow tubular portion at the pyloric extremity, the muscular tunics at this point acquiring a considerably increased thickness. Internally the secreting membrane is distinguished by irregularly disposed longitudinal folds, slightly elevated above the surface and intercommunicating by smaller rugæ of the same nature, having an oblique or transverse direction. There are no papillary eminences like those in the reticulum and manyplies, the lining membrane being soft, highly vascular, and occupied by the follicular openings of true gastric glands as in the human stomach. At the pylorus, in addition to the ordinary narrowing usually found at this part, there exists a special valvular process, developed from the mucous membrane at the commencement of the duodenum; in the Giraffe this protecting fold is situated just within the stomach (Owen). In the akeratophorous Ruminantia the reed is relatively smaller than in the horned species; in other respects it offers no appreciable difference.

The *ruminating function* is characterised by the following phenomena: — The food, on being received into the mouth, undergoes a very partial mastication, and in this crude state is speedily carried down the œsophagus, where, on arriving at the lower part, the lips of the muscular channel, placed at the entrance of the three first stomachs, separate, so as to ensure its passage into the paunch, In like manner, subsequent to the act of drinking, the margins of the œsophageal groove open, and the water is conveyed into the cells of the reticulum. In the Camels a proportion of the fluid passes into the first cavity, there to be retained by the great water-pouches, as a special provision against those contingencies which their mode of existence involves. While the coarse vegetable ingesta are being macerated by the moisture secreted from the walls of the rumen (and probably also from the water taken in by the mouth, some of which may have entered the cavity), portions of the indigestible mass are transmitted into the second stomach for further maceration, and from thence into the demi-canal, to be moulded into the form of pellets, and returned to the mouth by a kind of reversed peristaltic action. The softened bolus, thus brought back into the mouth, is destined to receive a thorough and deliberate remastication, and it is somewhat singular that this part of the process (called "chewing the cud") varies in different species. Professor Owen has the merit of showing that in the Cameline ruminants the bolus is triturated alternately from side to side, whereas, the action of the teeth in the horned Ruminantia, including the Giraffe, is always in *one* direction—it may be from right to left or left to right — occasioned by the rotatory motion of the jaw. The necessary reduction of the aliment having been accomplished, it is again transferred to the stomach in a pulpy semifluid condition; but this time, instead of entering the first or second cavities, it passes directly along the (now closed) œsophageal groove into the manyplies. Here, the superfluous moisture is supposed to be absorbed before it is ultimately transmitted into the fourth stomach, in which organ the true digestive act remains to be fulfilled. The first, second, and third stomachs are incompletely developed in the newly born individual, where no chewing of the cud taking place, the food passing directly into the fourth; in the Calf a peculiar organic acid is secreted by the lining membrane of the reed, which possesses the power of converting the albumen of milk into *curd* and *whey:* this, in the prepared condition, is termed *rennet.*

Concretions are frequently found in the paunch, and occasionally in the reticulum, composed of various substances, such as hair, vegetable tissues, or calcareous matter, having a more or less rounded figure. The balls, so common in the Calf and Cow, result from the licking of their own hides or that of others, — the hair thus collected being rolled into the characteristic shapes by a kind of felting process going on in the stomach; after a time they become coated with a dark earthy deposit of great hardness, the surface acquiring a considerable polish. Sometimes they have the form of compressed spheres, but are more usually barrel-shaped; their size is seldom larger than a cricket-ball. There is a specimen from the Cow in the Edinburgh University Anatomical Museum (presented by Dr. Mc Nab, of Jamaica), measuring eleven inches in length and twenty-nine in circumference. The fibrous concretions in the Camel consist of numerous small pedunculated pellets, strung together in botryoidal masses; at least, such is the form presented by those we have seen from a Dromedary dissected by Professor Goodsir. The formation of the so-called *Bezoar stones* in the stomach of the Chamois takes place in

Fig. 361.



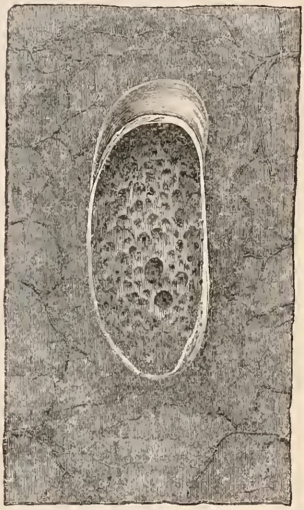
Intestines of the Sheep.

consequence of a partiality for saline matters, which the animal gratifies by licking portions of rock containing saltpetre; in this way, silicious and other earthy particles swallowed at the same time, accumulate and adhere together in the form of calculi.

The *intestinal tube* is remarkable for its length; in other respects its characters are for the most part extremely simple. Taking the Sheep as a type, we observe the descending or duodenal portion (*a*, *fig.* 361.) to be short and straight, but rather thicker than the remainder of the small intestine, which is twisted into a multitude of gyrations until within a short distance of its termination, where the convolutions cease, and the gut ascends in a direct line to join the colon (*b*, *fig.* 361.). The large intestine is scarcely broader than the small throughout the greater part of its extent; nevertheless, it is very much expanded at its commencement, and also a little dilated at the rectum (*d*, *fig.* 361.). The central mass of the colon folds itself into a series of double concentric circumvolutions, which are within one another, but not exactly on the same level, the inner coils being the most prominent; from this peculiar disposition it follows that the fœces are at first directed concentrically inwards and subsequently reversed excentrically outwards. The arrangement of the intestines in the Cameline ruminants differs little from the ordinary type: in the Llama the duodenum is enlarged at its origin, and further characterised by a short oval pouch, placed anterior to the first duplicature of the gut (Cuvier). The elongation of the digestive tube, as compared with the animals' length, from mouth to anus, may be reckoned, according to Meckel, as 12 to 1 in the Camels, Antelopes, and Deer; 22 to 1 in Oxen; and 28 to 1 in Sheep. The proportionate length of the large and small intestine also varies considerably; thus, while of equal length in Camelidæ, the smaller doubles that of the larger in Cervidæ, and is fully five times greater in Œgosceridæ, Antelopidæ, and Bovidæ (Meckel). The entire length of the intestinal canal in one of the Giraffes dissected by Prof. Owen, exceeded 134 feet. The *cæcum* (*e*, *fig.* 361.) is in all species bulky, and, like the colon, smooth and unprovided with lateral bulgings; its blind extremity is more or less obtuse, rounded, or club-shaped.

The *intestinal glands* in Ruminantia generally do not offer any deviation worthy of notice; in the Giraffe, however, we have discovered a curious exception to this rule, arising out of the presence of certain pouch-like folds in connection with the glandulæ agminatæ, and in particular with a very remarkable extension of the last Peyerian patch beyond the ileo-colic opening.* Probably more than one half of the entire series of agminated follicles exhibited this peculiarity, but in consequence of our having retained only some six or eight feet of the gut for minute examination, we are not in a position to state with accuracy either the total number or precise localization of *all* the glands (four of which were found) presenting this anomaly. In the small intestine the fold consists simply of a semilunar valve-like production of the mucous membrane, overlapping the anterior or duodenal end of each patch*, so as to leave a sort of cul-de-sac, the exposed or convex surface partaking of the ordinary villous texture, and the internal wall or concavity becoming follicular; it is conspicuous when distended, and leaves a fossa capable of admitting the tip of the little finger (*fig.* 362.).

Fig. 362.



Peyerian patch from the Giraffe, showing a valvular fold at one end. Natural size. (Original.)

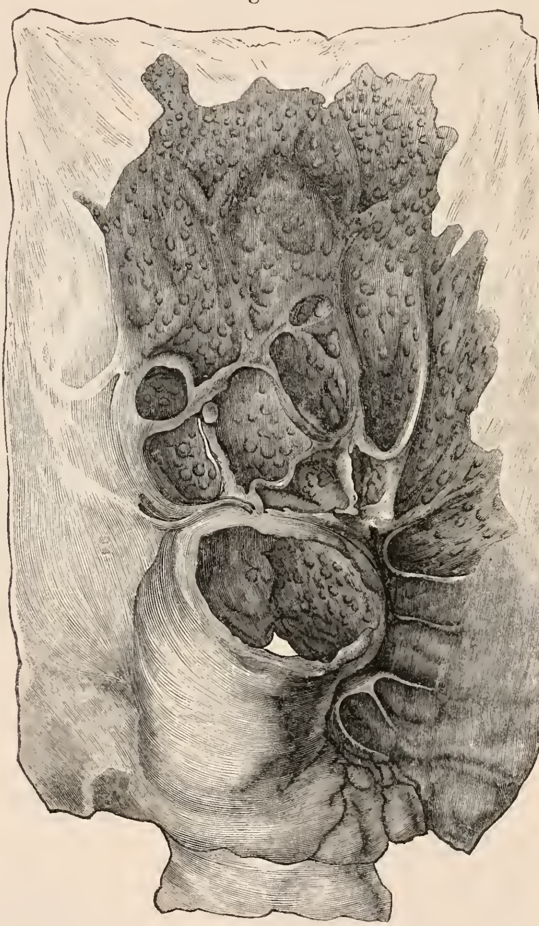
Far more striking and complicated is the pouched structure situated within the cœcal extremity of the colon (*fig.* 363.). Here, we have from fifteen to twenty sacculi combined to form a beautiful network of cells, seven of them resembling in many respects the water reservoirs of the reticulum, and having a depth which varies from three to four lines; the remainder are more or less incomplete, and those farthest from the ileo-colic orifice are mere depressions, the walls of separation being scarcely elevated from the surface. With the exception of two minute fossæ to the left of the valve, and three rather larger below, towards the cœcal extremity of the gut, the entire mucous membrane, both within and without the pouches, is beset with follicles having precisely the same character as those of the last Peyerian patch, of which indeed they are, in reality, a continuation;

* On a remarkable pouched condition of the *Glandulæ Peyerianæ* in the Giraffe. By T. Spencer Cobbold, M.D., Edin. Philosoph. Journal, New Series, vol. iii. 1856.

* Possibly the position here given is incorrect, as the intestine had been divided into sections before the structure was detected, rendering it difficult to decide this point with certainty.

for, not only do the follicles extend to the ileo-colic opening, but the intervening upper lip of the circular valve is likewise glandular. A few of the cavities are subdivided by secondary lamellæ, but generally speaking these are not very prominent. The larger folds, which contain muscular fibres of the non-voluntary kind, are extremely thin, transparent and extensile, so that the amount of secreting tissue is much greater than is at first sight apparent; in one example, to the left of the figure, the orifice of the saccule is much contracted, while the cavity on the other hand is particularly capacious. Altogether, without taking into consideration the laminated foldings, the follicles within the colon cover a space equal to about two square inches. We were unable to determine the length of the other division of the patch proper to the ileum, the intestine having been cut across too near the valve; its longitudinal extension may have been five or six inches; transversely, it occupied nearly the whole calibre of the tube.

Fig. 363.



Sacculated compound gland in connection with the ileo-colic valve of the Giraffe. Natural size. (Original.)

The *liver* is exceedingly simple, of small size, and wedge-shaped; it is thick at the anterior and right borders, and very thin at the lower or posterior margin. The lateral lobes are only indicated by a slight fissure at the entrance of the suspensory ligament, dividing the gland into two unequal halves,— that of the right being paramount and frequently developing a minute lobular appendage posteriorly. In the Giraffe it is elongated, compressed, and slightly cleft, so as to indicate a bilobular tendency: on the under surface there is an elevation corresponding to the lobus spigelii, the outer edge of which is particularly conspicuous. The entire gland in the Edinburgh specimen weighed only five pounds and six ounces, and measured in the long diameter sixteen inches — nine transversely, and but two and a half in thickness. The Camels have the under surface and inferior border characterised by a multitude of polygonal lobules, which are minute and varying in size, but circumscribed by rather deep grooves. This family, in common with the Cervidæ proper, is further distinguished by the absence of a gall-bladder, whereas the hollow-horned Ruminantia invariably possess this structure. In connection with this subject, Prof. Owen has pointed out a most curious anomaly in the aberrant cervine genus Camelopardalis. Out of three individuals anatomised by him, and a single specimen by ourselves, in one instance only has there been found a bile-cyst — a circumstance serving to illustrate a feeble alliance with the Antelopidæ on the one hand, and a near approach to the Cervidæ and Camelidæ on the other. The gall-bladder, discovered by Prof. Owen, occurred in a female Giraffe; it was bifid at the fundus, and exhibited several peculiarities which he has thus described.* "It was at-

Fig. 364.

Double gall-bladder of the Giraffe. (From Owen.)

tached in the usual manner and situation to the under part of the liver, having a covering of peritoneum over three-fourths of its surface. It measured three inches in length, and two inches in diameter. On making a longitudinal incision down one side of this apparently single gall-bladder, it was seen to be divided throughout its length by a middle vertical *septum*. Further dissection of this septum showed that the gall-bladder in fact was double, and that the two reservoirs of equal size were connected together, side by side, by means of a common investment of serous membrane. The lining membrane of each bladder was smooth; they communicated separately with the commencement of a single cystic duct, the terminal orifices admitting freely the blunt end of a common probe, and being protected by a valvular fold."

* Memoir, *l. c.* p. 228.

The hepatic duct attains an enormous size in the Sheep, and in this animal as also in the Ox and Goat, the common *ductus choledicus* enters the duodenum about twelve inches from the pylorus. The opening is a little less than eight inches distant from the stomachal orifice in the Camel, — and in the Llama, Deer, and Antelope, is situated quite close to the valve (Cuvier, Meckel).

The *pancreas* is somewhat bilobed, and, like the liver and spleen, comparatively insignificant. The excretory canal is spacious in the Sheep, and unites with the common duct of the liver about two inches from the duodenal communication; its junction takes place rather closer to the gut in the Camel. These passages are separate in the Ox, and sometimes leave a considerable interspace between their duodenal terminations.

The *spleen* usually presents a flattened oval or rounded figure; in its normal position it is applied against the left side of the paunch, and has about one-sixth of the weight of the liver. In the Llama its form is semilunar, and it is particularly narrow in the Antelopes, Deer, and Giraffe. On making a section through the spleen of the Ox, the malpighian corpuscles are seen to be remarkably large and conspicuous.

Organs of circulation.—The *heart* of the ruminant as in other mammifera, lies parallel with the sternum near the middle line. Its capacity corresponds with the large bulk of the herbivorous quadruped, but the auricles are relatively small as compared with the ventricles; this feature is more noticeable in Cervidæ, and in the Giraffe, where the organ in its entirety is rather more elongated than in the Camels. One of the most striking peculiarities possessed by certain species of this order, in common with many other animals, such as the Hog, Elephant, and Horse, — consists in the presence of one or sometimes two small ossifications situated in the *septum ventriculorum* at the root of the aorta; these so-called "bones of the heart" are flattened, more or less curved or cruciform, and generally speaking they are less strongly developed in the female; in the Giraffe this bone is about two-thirds of an inch in length (Owen). The distribution of the great vessels proceeding from the base of the heart resembles for the most part that of the human subject, but the *aorta*, as in Pachydermata, divides close to its origin into two unequal trunks, the smaller passing forwards and representing the *arteria innominata*, and the larger curving backwards to supply the place of the descending trunk. The ascending vessel gives off the *subclavian* artery much nearer to the heart in Solipeda than in the Ruminants (Meckel). In the Bactrian Camel the subclavian is not quite so far distant as in the Horse, while in the Dromedary this division leaves the *innominata* within two lines from its insertion into the heart (Daubenton). The deviations of the *vertebral* were indicated when describing the characters of the cervical vertebra in the different genera. The thyroid body is supplied by the *inferior thyroideal* only, the *superior* being distributed to the larynx. In the fore-limb, a vascular twig, corresponding to the *interosseous artery*, is present both in the Ruminants and Solipeda; it is very voluminous in the former, and but faintly marked in the latter. The *common carotids* are remarkable for their length in certain individuals; the most interesting peculiarity, however, obtains in the presence of numerous anastomising branches given off by, and tortuously inter-communicating between the internal carotids. It is this plexus which has been long known under the name of *rete mirabile*, being situated within the cavernous sinus on either side of the sella turcica, and occasionally extending backwards to join the vertebral artery. Similar appearances are found in Carnivora, and in Cetacea where they are are not confined to the region of the cranium; many other anomalies of the same kind occur in other families, the most striking being seen in the Sloth, where the *brachials* and *femorals* are split up, as it were, into numerous hair-like capillaries. The *spermatic artery* is exceedingly large in the Bull and twisted into a multitude of convolutions. In regard to the *venous system* of ruminants we have only to remark that, according to Weigel, valves are developed in the *portal vein.**

Organs of respiration. — The structural modifications observable in this system depart so slightly from the ordinary mammiferous type as scarcely to call for a separate notice. The organisation of the *larynx* is simple, its anterior ligaments and ventricles being absent; in many species the thyroid cartilage is comparatively narrow. The tracheal rings are for the most part incomplete, and vary numerically in accordance with the length of the neck. According to Meckel there are fifty in Moschus; sixty in the Stag; seventy in the Chamois, Ox, and Sheep; eighty in the Llama; and upwards of a hundred in the Dromedary. We have counted ninety-two in the Giraffe, where the length of the trachea is between four and five feet; in this genus the epiglottis is short and thick, and the arytenoid cartilages are remarkably large and prominent, as in Ruminantia generally. Occasionally there are three primary bronchial subdivisions; when the trachea is simply bifurcated, the right bronchus is paramount. Most ruminants have the lung of the right side separated into four lobes, and the left into two; in the Camel the right pulmonary organ is double, while the left is single, and exhibits no subdivision. The *thymus gland* is extensively developed in this order and prolonged forward on either side of the trachea.

Nervous system. — The *brain* is elongated, and more or less oval-shaped; it is narrowed anteriorly in the Sheep, and somewhat abrupt in this direction in Cervidæ (*fig.* 365.). Con-

Fig. 365.

Brain of the Giraffe. (From Owen.)

sidered in reference to the bulk of the animal the brain is significantly small in this order, as in Pachydermata and Solipeda. Its weight in the Ox is only one-fourth of the human brain, although the body of the former is six times larger than that of the latter; virtually, therefore, the brain in Man is twenty-four times greater than in the Ox (Monro). The proportionate weight of the cerebrum as compared with the *cerebellum* and *medulla oblongata*, is likewise less considerable in ruminants generally than in the human subject. The cerebral convolutions are numerous and tolerably

* Weigel, de strato musc. tunicæ venarum mediæ, etc., p. 31. Leips. 1823.

symmetrical as in the Horse; the cerebellum is divided into several irregularly disposed lobules of variable size.* The base of the brain is more flattened than in Man. In the Giraffe the cerebrum lies on the same level as the cerebellum, and does not overlap it (*fig.* 365.). The anterior pair of the *corpora quadrigemina* are paramount in most if not in all the species. The *corpora mammilaria* are of considerable size. The lateral ventricles intercommunicate. All the nerves at the base of the cerebrum are conspicuously large, especially the olfactories, which form broad bulbous expansions in front, where they are applied to the cribriform plates of the ethmoid bone. The *spinal chord* and *nerves* are chiefly remarkable for their length in certain genera; in the Giraffe the filaments entering into the composition of the anterior and posterior nervous roots of the chord, are widely separated from one another at their origins.

Organ of vision. — In common with many other quadrupeds, ruminants are provided with an *Harderian gland;* it is situated at the inner angle of the eye, and opens by a single duct behind the so-called *membrana nictitans* or third eyelid. The *glandulæ lacrymales* are lobulated. The eyeballs are placed wide apart, and are particularly prominent in Camelidæ and in the Giraffe, enabling these animals to look straight in a backward direction without turning the head. The pupillary aperture is oblong transversely, as in Cetacea and Solipeda, the latter family having flocculent masses developed from the *uvea* which project into the anterior chamber. The most striking feature of the ruminant eyeball arises from the presence of a *tapetum*, provided with an extremely brilliant metallic lustre, varying in tints of yellow, green, blue, violet, and purple.

Organ of hearing. — The essential part of the auditory apparatus is similar in construction throughout the entire mammiferous series; but the external auricular appendages are largely developed in Ruminantia, and moved by a numerous and complicated set of muscles: these have already been referred to. Internally, a small sessamoid bone is sometimes found in connection with the stapedius muscle of the Ox. In ruminants generally, the *cochlea* scarcely exhibits the same amount of turning as in man, the number of coils being rather less than two and a half; in the Chamois only two whorls are present. Minor differences exist in the form of the semicircular canals; in the Camelidæ and Capreæ their curvature is elliptical, and in Antelopidæ it forms the segment of a spiral; in Solipeda the curve is parabolic. In the first of these families the canals are particularly spacious. The *tympanum* in Bovidæ is irregular in form, and made up of numerous cells; — these are absent in Œgosceridæ, where the cavity is farther distinguished by its capaciousness.

Organ of smell. — The olfactory sense is very highly developed in the present family, but the organic modifications are unimportant, except in so far as they refer to a corresponding structural increase. An interesting and special provision, however, is formed in the Camel for the protection of the schneiderian membrane from the injurious effects of the *tornado*, during which, particles of sand are driven along the deserts with great violence; the nasal aperture instead of being patent, assumes the form of a narrow cleft, and to ensure its temporary closure, a subcutaneous sphincter muscle is placed at the entrance, subject to the control of the animal's will; under ordinary circumstances the nostril is well guarded with stiff bristly hairs. The openings of the cribriform lamellæ of the os ethmoides are particularly large, and the inferior turbinated bones are enormously developed and folded longitudinally into several gyrations. In most species the nasal, maxillary, and other cranial sinuses are very extensive.

Urinary organs. — The only peculiarities worthy of remark under this head have reference to the imperfectly lobulated character of the kidneys in Bovidæ, and the large size of the urinary bladder in ruminants generally, the latter feature being a characteristic of all herbivorous quadrupeds. The glandular bodies situated towards the inner side of the renal organs are more or less oval and elongated.

Reproductive system. — The *male sexual organs* exhibit few departures from the ordinary mammiferous type. The *testes*, as in Solipeda and Man, are enclosed within a scrotum, which is pendulous, and divided by a thin cellular septum. The gland itself is invariably egg-shaped, its longitudinal extension being considerably increased by the projecting *epididymis* above and the *globus major* below. It is more significantly characterised by the presence of a *corpus highmorianum*, which is essentially a production of the *tunica albuginea*, traversing the organ lengthways, and giving off numerous aponeurotic bands, — the latter radiating inwards between the seminal tubes and separating them into lobular bundles. The *tunica vaginalis* is continuous with the abdominal cavity. The *vesiculæ seminales* are largely developed, and exhibit two lateral horns which have a globular form in Œgosceridæ and Cervidæ. These lobes are by some described as *prostatic;* but others regard a narrow glandular layer, lying immediately in front of the above, as the representative of the last-named structure. In the Ram the *vasa deferentia* unite near

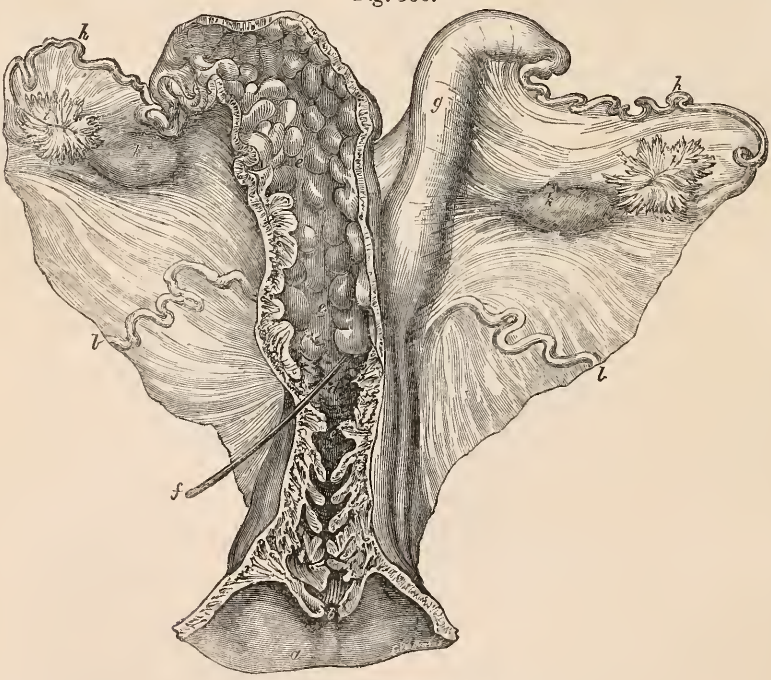
* The design and scope of the present article forbid our entering minutely upon the Comparative Anatomy of the Brain and some other organs of special interest. We cannot, however, quit this part of our subject without referring to the important Memoirs of M. Camille Dareste, in the *Ann. des Sc. Nat.*, on the "Convolutions of the Brain in Mammifera," and more particularly to his third Memoir (No. 2., tom. iii., série iv.). In this paper M. Dareste shows that the complicated arrangements exhibited by these organs in the different ruminant families, may be all reduced to a simple type,—and this typical condition he has beautifully illustrated (in his second Memoir) by a description of the actual appearances found in the brain of the Javanese Musk.

their terminations to form a single common duct. The *glands of Cowper*, placed behind the urethral bulb are rounded and conspicuous. The *penis* is long and usually bent upon itself, in the form of the letter *s* a little anterior to the bulb. In some genera the *glans* is apparently very small in consequence of its attenuation, as in the bull. In all cases the canal of the urethra ends in front by an extremely narrow whip-like process of the *corpus spongiosum*, reminding us of the modifications of this organ in certain mollusks. The *prepuce* is prolonged forward in the form of an elastic sheath, which in the Giraffe is so closely adherent to the bulbous root of the glans, as to be with difficulty separated ; by putting the parts a little on the stretch, we have found the reflection fully two inches posterior to the glans. Preputial follicles abound in the Antelopes and Cervidæ, and in the Musk-deer there is a special glandular pouch communicating with the cavity of the prepuce by a single duct ; it is from this structure that the substance *musk* is derived.

Female organs. — Generally speaking the *ovaria* (*k*, *fig.* 366.) and *fallopian tubes* (*h*) have the same relation to each other as in other mammifera, but differences exist in regard to the connection of these parts with the broad ligaments in the cameline and horned ruminants severally. They have been indicated by Prof. Owen as follows.* — " In the Camel the greater part of the *capsula ovarii* is formed by the expanded fimbriated aperture of the oviduct itself, which is of very large size, and which encloses the ovarium, In Deer, Antelopes, and Cows, the ovarium is lodged in a depression or *sacculus* of the broad ligament, which is more or less deep, and has its apertures more or less contracted in different species. In the Giraffe the *peritoneal sacculus* of the ovary, formed by an expansion of the broad ligament of the uterus, is wide and deep, and encloses almost the whole of the ovary. The fimbriated extremity of each oviduct, or fallopian tube, is expanded upon the outer margin of the ovarian capsule. The inner surface of the pavilion is beset with very numerous and fine oblique *striæ*, and is further increased by narrow folds of *laminæ* converging towards the contracted opening duct. The oviduct forms three or four wavy folds, and is then continued along the walls of the wide *ovarian capsule* to the extremity of the uterine horn, which makes an abrupt curve to meet it."

In all ruminants, as in Solipeda and several other mammalian orders, the cavity of the uterus (*a*, *fig.* 366.) is prolonged superiorly

Fig. 366.



Uterus and its appendages, from the Sheep.

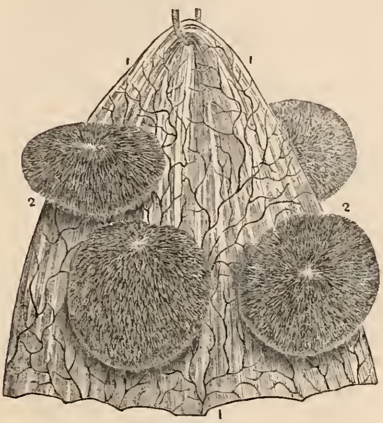
into two horns from the inner surface of which project a number of glandular protuberances (*e*, *e*, *fig.*366.). These processes are highly vascular, and exhibit eminences and follicular depressions for the implantation of the tufted filaments of the *cotyledons* or *placentulæ*. In the Camels, where the ovum is nourished, as in the Mare and Sow, by a villous chorion universally adherent to the uterine walls, these processes are not pre-

* Memoir, *l. c.* p. 241.

sent. In the typical species, numerous transverse and prominent rugæ are developed internally at the lower part of the uterine cavity; they are somewhat irregularly disposed in parallel rows, and are more crowded together towards the *os tincæ*, where they are split up, as it were, into fine longitudinal lamellæ, imparting to the *os*, when viewed from below, a peculiar radiated aspect. This latter feature is very striking in the Camels and in the Giraffe. The vaginal mucous membrane (*a*) is smooth throughout, and contracted inferiorly at the external orifice. In horned Ruminantia the *clitoris* is placed just within the *vulva*, but external to the vaginal outlet in the Camelidæ (Owen). Preputial follicles also occur in the female ruminant as well as Cowperian glands, which are situated near the root of the clitoris.

In the *gravid uterus* of the typical species, the fœtal membranes — consisting of the *chorion* (1, *fig.* 367.), *amnion*, and *allantois* —

Fig. 367.



Portion of the chorion of a Cow, showing the cotyledons. (*From Gurlt.*)

are connected to the walls of the cavity by numerous small *placentulæ* or *cotyledons* (2, *fig.* 367.), which embrace and dove-tail with a corresponding series of processes developed from the uterus. The cotyledons are productions of the chorion, and have an oval or rounded shape, more or less compressed, the exposed surface being usually cup-shaped; after the expulsion of the fœtus these bodies come away with the membranes, and the uterine protuberances diminish considerably in size. In the Sheep and Cow the number of the placentulæ varies from about seventy to a hundred. Like the *chorion*, the *amnion* is highly vascular. The *allantois* exists in the form of a closed sac, and only partially covers the amnion. In the Cameline ruminants the ovum is retained in situ by a universally adherent villous chorion, such as is found in Solipeda and Pachydermata.

The *mammary glands* are situated in the inguinal region between the thighs; the *teats* are four in number, except in Œgosceridæ, where there are only two. Rudimentary nipples are occasionally found in the male on either side of the scrotum; in the Horse they exist on the sheath of the penis.

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T. Spencer Cobbold.

UTERUS AND ITS APPENDAGES.

—The reproductive organs in woman consist of the Ovaries, Fallopian Tubes or Oviducts, Uterus, Vagina, and Vulva. These are commonly subdivided into the *formative* and *copulative* organs. To the first division belong the ovaries, Fallopian tubes, and uterus; to the second the vulva; while the vagina, on account of its offices in copulation and in labour, may be regarded as common to both.

This division nearly corresponds with another and more artificial arrangement, by which these parts are subdivided into the internal and external generative organs; those being regarded as internal which are protected within the body and concealed from view, while those which can be easily seen are termed external: the line of demarcation being here at the entrance to the vagina.

Of the several organs just enumerated, the uterus has doubtless, on many accounts, prior claim to attention. It is the largest of these parts. It is that which contributes the greatest amount of material to the new organism which it contains and protects. It is that part in which alone a direct connection of attachment subsists between the fruit and the parent. Its functions, so far as they contribute to each individual act of reproduction, are exercised for much longer periods of time than those of any other portion of the generative apparatus. It exerts a powerful reflex influence, especially during pregnancy, upon other parts and organs. The diseases and accidents to which it is liable are more numerous, and are attended by greater danger to life than those which affect any other portions of these structures, whilst its several morbid states, as well as its natural condition, may be ascertained during life with a degree of precision which virtually removes the uterus from the category of internal parts.

But it is only in a practical or obstetric point of view that the uterus can be regarded as the most important of the generative organs. Physiologically considered, it is by no means entitled to the foremost place; for although the presence of the uterus is necessary to the completion of the generative act in its regular course, yet reproduction to a certain extent may be accomplished without it. The uterus is necessary to reproduction, first, as affording the only channel by which the seminal fluid can obtain access to the ovum; and next, as constituting, together with the vagina, the only natural passage for the exit of the fully matured ovum, which requires this contractile organ to effect its expulsion by that passage: such expulsion not being essential to the generative act because the fœtus may be extracted by the Cæsarean section without necessary loss of life either of the parent or offspring, while other parts—the Fallopian tubes for example—may, to a certain extent, perform the offices of a uterus in all that relates to the protection and nutrition of the ovum. Moreover, the entire removal of the uterus may have no other effect upon the individual than that of preventing impregnation and menstruation by the simple abstraction of the parts necessary thereto.

On the other hand, the ovary, though constituting only a small portion of the reproductive organs, is nevertheless that part to which all the rest are subservient. It is the organ which furnishes the generative element essential to the reproductive act. It is that part which, in a great measure, regulates the growth of the body, and determines the distinctive characters of the sex. It is the organ upon the presence of which depends the sexual passion and the process of menstruation; whose congenital deficiency is indicated by the absence externally of all signs of a secondary sexual character; whose artificial removal entirely unsexes the individual, and the decline of whose functional activity, as age advances, is the cause of the generative faculty being lost in the female long before the ordinary term of life has expired, and at

Fig. 368.

Fig. 368.

Uterus and appendages of an adult virgin, posterior aspect. (*Ad Nat.*)

a, uterus; *bb*, ovary; *cc*, Fallopian tube or oviduct; *dd*, fimbriated extremity or infundibulum of the tube; *ee*, terminal bulb of the duct of Müller; *ff*, portion of broad ligament and blood-vessels; *g*, vaginal portion of cervix uteri; *h*, os uteri externum; *i*, anterior and *l*, posterior wall of vagina; *m*, ligamentum ovarii; *n*, tubo-ovarian ligament.

a much earlier period than that at which the power of procreation ceases in the other sex.

In a physiological sense, therefore, the uterus, as well as every other part of the generative apparatus, must be regarded as an appendage of the ovary; and the title "Uterus and its Appendages" is employed, in accordance with ordinary usage only, as the heading of this Article, in which it is proposed to consider the structure and functions of the entire female generative organs as they exist in Man.*

OVARY.

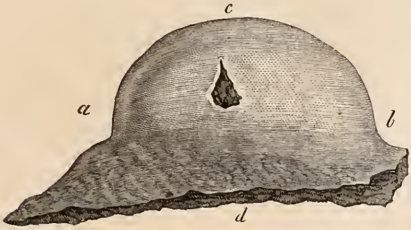
NORMAL ANATOMY.

(SYN. *Ovarium*, *Testis Muliebris*, Lat.; *Ovaja*, Ital.; *Ovaire*, Fr.; *Eierstock*, Germ.; *Eijerstok*, Dutch.)

The ovaries (*fig.* 368. *b*, *b*) constitute two follicular glands appropriated to the formation of the female generative element. They are perfectly closed, resembling in this respect the ductless glands. Each, however, is furnished with its proper excretory duct, (*fig.* 368. *c*, *c*) between which and the gland a temporary connection is established, at certain intervals, during that period of life over which the reproductive faculty extends.

Form. — The ovary is not usually fully developed until some time after the establishment of puberty. It is then of an oval form

Fig. 369.



Ovary of a young adult virgin before the surface has become scarred by repeated discharges of ova. (*Ad Nat.*)

a, distal, and *b*, proximal extremity; *c*, superior, and *d*, inferior border. In the centre is laid open a Graafian follicle from which an ovum had recently escaped by spontaneous rupture.

(*fig.* 368. *b*, and *fig.* 369.), flattened on its sides, and somewhat resembling the testis in figure, but rarely or never, in a state of health, attaining to the full size of that organ.

The following division may be made of its superficies: viz., into two sides, situated anteriorly and posteriorly with regard to the body; two extremities, outer and inner; and two borders, superior and inferior.

Of the two sides, that which is directed anteriorly (*fig.* 370. *e*) is both shorter and less

Fig. 370.

Vertical section of ovary. (*Ad Nat.*)

The posterior surface, *f*, more rounded than the anterior, *e*; at *h* are numerous blood-vessels divided; *gg*, Graafian vesicles; *d*, place of entrance of vessels between the layers of the broad ligament.

convex than the posterior, which is generally rounded and gibbous (*fig.* 370. *f*). In this respect the ovary resembles the uterus, whose posterior surface is always more rounded than the anterior; by attention to this peculiarity the right ovary may be readily distinguished from the left after these organs have been detached from the uterus.

Of the two extremities, the outer or distal (*fig.* 369. and *fig.* 372. *a*) is usually rounded and bulbous, whilst the inner (*figs.* 369. and 372. *b*) becomes gradually attenuated until its outline is merged in the proper ligament (*fig.* 368. *m*) by which the ovary is attached to the uterus. The upper and lower borders also differ from each other. The former (*fig.* 369. *c*) is convex, and forms a segment of a circle, whose diameter is continually diminishing as age advances. The latter is straight or slightly concave, constituting the base of the ovary, or the line by which it is connected to the posterior duplicature of the broad ligament (*figs.* 369. and 370. *d*).

Dimensions and Weight. — The ovary of a healthy adult measures from 1″ to 2″ in length, from 6‴ to 12‴ in depth or perpendicular diameter, and from 3‴ to 6‴ in width or transverse diameter.

These dimensions, which vary considerably in different individuals, exhibit a much wider range when the observations are extended to different epochs of life. The organ is then found to undergo far more remarkable changes in bulk and figure than are observable in the corresponding male organ.

The following table, giving the highest, lowest, and mean dimensions of twelve healthy ovaries, taken indiscriminately from women in various conditions during the period of fertility, will serve to exemplify the first of these variations: —

* For the comparative anatomy, as well as for the general treatment of the subject of generation, the reader is referred to the articles, GENERATION, ORGANS OF; GENERATION; and to those descriptive of the different classes and orders of the animal kingdom throughout this Cyclopædia. The occasional introduction here of illustrations from comparative anatomy and physiology is employed for the purpose of elucidating those questions which cannot be clearly explained by observations made only upon the human subject.

	Longitudinal.	Perpendicular.	Transverse.
Highest	2″	1″ 1‴	6‴
Lowest	1″	6‴	3‴
Mean	1″ 4‴	9‴	4½‴

Another and more accurate method of estimating the bulk of the ovary consists in weighing. The following are the extreme and mean weights of five ovaries taken from healthy adults: viz., greatest weight, 135 grs.; least, 60 grs.; mean (of five examples), 87 grs. On comparison of these results with Krause's estimate of the weight of the testis, which gives the mean weight of the male organ, also in five instances, as 354·4 grs.*, it appears that the ovary, though furnishing the larger portion of the generative element in the act of reproduction, has an average bulk of less than one quarter of that of the corresponding male gland.

Position and Connections.— The ovary is so intimately connected with the uterus, in whose changes of position, both normal and abnormal, it necessarily takes part, that it cannot be said to have any fixed or definite seat. It is most commonly found lying somewhat deeply in the lateral and posterior part of the cavity of the true pelvis, concealed from view by the small intestines, and in part covered by the Fallopian tube of the same side. Relatively to the uterus, the ovary is placed on either side of that organ, at a distance varying from 4‴ to 18‴, and behind and a little below the level of the point of entrance of the Fallopian tubes (*fig.* 368.).

Each ovary is invested by a layer of peritoneum derived from the posterior lamina of the broad ligament, to which the ovary is thus attached by a kind of mesentery.

Besides this indirect connection with the uterus, through the intervention of the broad ligament, the ovary has also another and more direct attachment by the aid of its own proper ligament (*ligamentum ovarii*), which serves to bind it more securely to the uterus. (*Fig.* 368. *m*.)

The ovary is further connected at its outer extremity to the mouth of the Fallopian tube by one of the processes of the pavilion, which serves to keep the organ always in close proximity to its excretory duct (*fig.* 368. *n*).

The distance which intervenes between the ovary and the uterus varies considerably on each side, not only in different individuals, but also in the same subject, where it is very rarely found to be equal; the right ovary, so far as my observations have gone, being farther removed than the left in the proportion of nine out of twelve instances.

During pregnancy, the ovary suffers frequent changes of position. As the uterus expands, it carries the ovary along with it into the abdominal cavity, at the same time the relative situation of these parts is materially altered, the fundus uteri gradually expanding and rising above the former level of the ovaries, whilst the latter appear to be bound down more closely to the side of the uterus, until at term their position is usually found to be below the centre of that organ.

Component Parts. — The ovary is composed of, 1st, protecting parts, or tunics; 2nd, a parenchyma, or stroma, in which are imbedded; 3rd, the proper secreting structures, in the form of closed sacs or vesicles, containing the ova; 4th, vessels and nerves.

1. *The Protecting Parts or Tunics.*—These are two in number, and correspond precisely, both in structure and derivation, with the analogous coverings of the testis.

The peritoneal covering (*fig.* 371. A) constitutes the outermost of these coats, and consists of the layer of peritoneum derived from the posterior lamina of the broad ligament, which serves to connect the ovary with the parts adjacent. Except at its base, the ovary is so closely invested by this peritoneal lamina, that no effort with the scalpel will suffice to detach it from the tunic beneath. This intimate union, however, of the two coats ceases at the base of the ovary, where a white, irregular, and somewhat elevated line is observed on either side, extending in a horizontal direction, and rising higher on the anterior than on the posterior surface of the gland. In its intimate texture, this covering of the ovary differs in no respect from the peritoneum covering the viscera generally.

The tunica albuginea, or *tunica propria*, (*fig.* 371. BB) constitutes the special or proper covering of the ovary. It serves to give form and solidity to the organ, and to protect the ovisacs and ova from injury. This coat has a nearly uniform thickness of ⅓‴, and forms a complete investment for the ovary, except at its lower border, where the fibres are either very thinly scattered and interlaced, or are altogether wanting, leaving a longitudinal space, termed the hilum or vascular fissure, by which the vessels and nerves enter the organ. This space measures 3‴—4‴ in width, and extends along the entire base of the ovary.

The tunica albuginea has been commonly regarded as a more condensed portion of the stroma, or parenchyma, of the ovary; but from this it is readily distinguished, not only by its clear white colour, and dense and almost cartilaginous hardness, but also by its microscopic characters. On account of its extreme toughness, this tunic is not very easily separable into fragments sufficiently minute for microscopic examination. But when small portions have been so obtained, the margins of the fragments exhibit numerous close-lying and irregularly arranged fibres of developed connective tissue, projecting from a dense, structureless matrix interspersed with granules, which serves to connect the fibres together, and to which apparently is due, in a great measure, the peculiar toughness of this membrane, while its remarkable whiteness is

* See art. Testis, Vol. IV. p. 976.

explained by the much smaller number of blood-vessels that it contains, as compared with the general parenchyma of the ovary. The tunica albuginea, therefore, is not merely a more condensed form of the ovarian stroma, but appears to result from a development of tissues which exist in the stroma in an elementary or embryonic form, as well as from a more close conjunction and blending of those tissues.

2. *The Parenchyma or Stroma*, (*fig.* 371. C, and *fig.* 372. *s*) constitutes the proper tissue of the ovary. It lies immediately beneath the tunica albuginea, and fills up the whole of the intermediate space between the ovisacs, to which it acts as a germ bed, protecting the ova from injury, and serving for the conveyance of blood-vessels to the ovisacs. This tissue is sometimes of a pale-pink, but more often of a bright-red colour, from the large number of blood-vessels which it contains, whose arrangement proceeding from within, and radiating outwardly in all directions, gives to this tissue, when viewed by the naked eye or by

Fig. 371.

Ovary enlarged four diameters. (*After Coste.*) *Dissected to shew,*

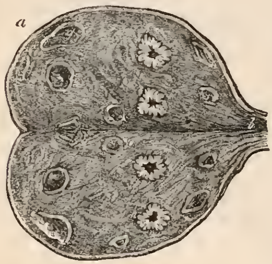
A, peritoneum; B, tunica albuginea; C, stroma; DDDD, Graafian follicles in various stages of growth; EE, outer coat of the follicle (tunic of the ovisac); FF, inner coat of the follicle (ovisac); GGG, epithelial lining (membrana granulosa); HH, ovum and cumulus; I, orifice by which the follicle has discharged an ovum; K, Fallopian tube; L, fimbriæ; M, posterior ala of broad ligament or mesentery of ovary; N, tubo-ovarian ligament; O, ligamentum ovarii.

a common lens, the appearance of being formed into bundles or laminæ.

The microscope, however, serves to resolve this tissue into its true elements. When so examined, the stroma is found to be composed mainly of blood-vessels, to which a great part of its strength and toughness is due, the intermediate spaces being filled up by a fibrous structure not separable into bundles, like ordinary connective tissue, and having no distinct fibrillar arrangement, its chief elements being single white fibres of ordinary connective tissue, numerous fusiform embryonic fibres, and elliptical and round cells or granules, the whole being coherent and strongly united together.

3. *The Graafian Vesicles. Folliculi ovarii, s. Graafiani, s. Ovisacci.*—When the substance of a healthy ovary is divided by a clean incision, if the subject be not too advanced in life, the section will be found to have included several vesicles varying in diameter from 4‴ down to sacculi of microscopic minuteness. These vesicles, familiarly known as the ova of De Graaf, although the credit of antecedent observation is certainly due both to Vesalius * and Fallopius †, are variously distributed through the ovary according to the age of the individual. In infants and young subjects, the ovisacs are found only at the periphery of the organ, where they form a thick rind, the interior of the ovary being occupied only by blood-vessels and stroma. But after puberty the division into a cortical and central part becomes less distinct, the ovisacs becoming buried deeper in the stroma, so that occasionally, in making sections of the part, they are encountered as deep as the base of the organ. They are always, however, most numerous near the surface.

Fig. 372.



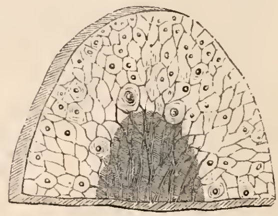
Longitudinal section of adult ovary. (*Ad Nat.*)

a, distal; *b*, proximal end; *s*, stroma; *g*, Graafian follicles of the ordinary size before enlargement; *h*, stellate remains of follicles which have burst and shrunk after discharging their ova.

The number of developed vesicles contained in each ovary, and visible to the naked eye, varies considerably in different subjects. Up to a very recent date it appears to have been assumed that their number was limited. They were usually estimated at 12 to 20 in each ovary; and it was generally supposed that, when these were exhausted by child-bearing and miscarriage, the power of procreation of necessity ceased. More recent and careful observation, however, has shown that the number of vesicles in each ovary amounts in healthy organs to 30, 50, 100, or even 200; whilst in very young subjects their numbers exceed all power of accurate computation.

The vesicles are most easily displayed in the adult ovary by making a perpendicular section through the organ in the direction of its longer axis. In this way the largest number will have been divided by one incision; and such a section, as in *fig.* 372., will often suffice to exhibit 8 to 12 vesicles of different sizes. On submitting the section, however, to the microscope, others of a smaller size, which had previously escaped attention, will be brought into view; and in continuing the incisions in various directions, fresh vesicles will be laid open of various sizes and in different stages of development. If the ovary of an infant be selected for observation, the organ should previously have been hardened by maceration for several days in spirit. A clean section is thus easily obtained by a sharp knife; and if this be examined by a 1-inch object glass, the little spherical ova, coagulated by the action of the spirit, will be readily seen, each one lying in its proper ovisac, by which it is immediately surrounded, and the whole so closely set and so numerous that a single section suffices to display several hundred of them at one view (*fig.* 373.).

Fig. 373.



Section of part of the ovary of an infant, aged 20 *months. The central portion consists of stroma and blood-vessels only. The lighter peripheral part is composed entirely of close-set ovisacs, containing ova of various sizes.* (*Ad Nat.* × 16 *diam.*)

The Graafian follicle, when not subjected to pressure from surrounding parts, or from adjacent vesicles, is spherical or oval in form, (*fig.* 371. DD, and *fig.* 372. *g*) and consists of certain tunics and contents. The number and composition of its coats have been variously described by recent observers; and upon this subject a difference of views would be of comparatively little importance, if upon a right solution of this question did not depend the clear comprehension of those changes which occur in the Graafian follicle during preg-

* De Corporis humani Fabrica, lib. v. cap. xv. p. 459.

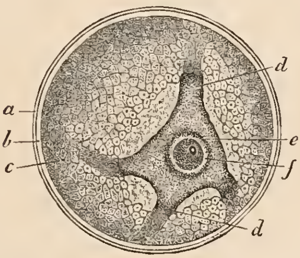
† Obs. Anat., Op. omnia, 1606, vol. i. p. 106.

nancy, and which result in the formation of the body termed the *corpus luteum*.

Without entering upon the question of the number of laminæ into which the walls of a Graafian follicle may be split by skilful manipulation, it will suffice to consider those only as distinct membranes or coats, which exhibit obvious differences of structure and relationship, during the various phases of development and decay which the follicle undergoes from its first formation to its final disappearance. In this view the walls of the Graafian follicle must be regarded as being composed of three membranes; and indeed but for the importance attached to the use of the third or innermost of these, which in any case is hardly more than a thin layer of granules, it would have sufficed if the coats of the vesicles had been enumerated as two only.

The external fibrous or vascular coat (*fig.* 374. *a*, *fig.* 371. E) constitutes the *tunic of the ovisac* of Barry, the *tunica fibrosa*, S. *theca folliculi* of Baer. It forms no portion of the original ovisac, but is a superadded part, derived from the parenchyma of the ovary. This coat closely embraces the ovisac, and partakes

Fig. 374.



Graafian vesicle of the rabbit × 100 (?) *diameters.* (*After Barry.*)

a, outer coat or tunic of the ovisac; *b*, ovisac; *c*, epithelial lining or membrana granulosa, a portion of which has been removed in order to display *dd*, retinacula (here too distinctly marked); *e*, tunica granulosa of Barry immediately surrounding the ovum, consisting of, *f*, zona pellucida, within which is the yelk and germinal vesicle and macula.

in its spherical figure; it carries numerous blood-vessels, which pass from the ovarian stroma to become expanded in a vascular network over its walls (*fig.* 371. D).

Examined by the microscope, this membrane is seen to be highly vascular. It is composed of a fine membrane, containing few fibres, but everywhere abundantly studded with oval nuclei, visible without the aid of acetic acid, and probably, in part at least, due to the presence of so many blood-vessels in its tissue. This coat contains no oil globules. Its chief use appears to be to give increased support and protection to the true ovisac which it surrounds, and to convey blood-vessels from the ovary for its nutrition, and for the supply of the fluids which the ovisac contains.

The second or internal coat, as it is commonly termed, of the Graafian follicle is the ovisac itself. It constitutes at first an independent structure; but receiving afterwards the before mentioned investment from the ovarian parenchyma, the two coats unite to form the Graafian follicle. The ovisac is.

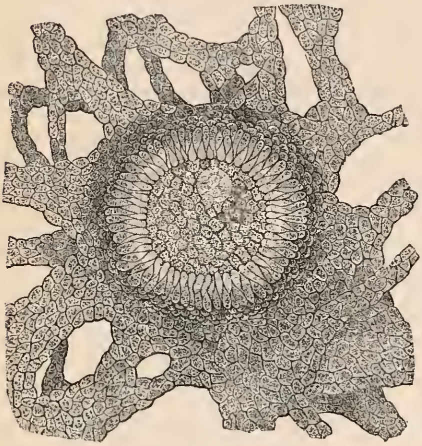
Fig. 375.

Structure of ovisac. (*Ad Nat.* × 350.)

composed of embryonic fibres of connective tissue (*fig.* 375. *a*), of rounded cells or granules, *b*; and of a large proportion of minute oil globules, *c*. The embryonic fibre-cells lie parallel with each other, and together with the granules form the bulk of the tissue in nearly equal proportions. The oil drops are very numerous; and after the preparation has been under examination for some time they are seen to float up to the surface of the drop of water in which it is placed, and to collect upon the under side of the glass disc used for covering it. In addition to these there is found a small quantity of developed fibres of connective tissue, which appear to give firmness to the whole. The Graafian follicle thus composed, contains, in close contact with its inner wall, a stratum of nucleated cells, forming an epithelial lining, termed the *membrana granulosa* (*fig.* 374. *c*, *fig.* 371. G). The cells or granules which give a name to this membrane are so lightly held together that it has been doubted whether the stratum which they form is really entitled to the denomination of a membrane. Nevertheless this structure appears to play an important part in regard to the ovum, which is always found lodged within a portion of it. At the commencement of the formation of the ovisac, according to Dr. Martin Barry, these peculiar elliptical nucleated cells or granules are nearly equally diffused through the fluid which it contains, the ovum lying in their centre. But about the time at which the ovisac unites with its covering or tunic to form the Graafian follicle, these granules are found to have become separated into little groups, leaving interspaces filled by fluid. Further, as this separation advances, the granules arrange themselves in such a manner as to constitute three distinct structures. The principal portion collects upon the inner surface of the ovisac forming the *membrana granulosa* just described (*fig.* 374. *c*). A second portion becomes aggregated upon and around the ovum, taking its form and constituting a special investment for it. This is the *tunica granulosa* of Barry (*fig.* 374. *e*). A third portion collects to form a structure composed of a central mass in which the ovum with its tunica granulosa is imbedded, corresponding with the *cumulus* (*fig.* 371. H, H) of Baer, and of certain cords or flattened bands, from two to four in number, which pass off from the central mass outwards, to become united with the layer of granules lining the follicle. These radiating bands or cords are termed by Barry the *retinacula*, (*fig.* 374. *dd*) from their supposed office in suspending the ovum, and retaining it in its proper situation in the Graafian follicle.

That the *retinacula*, however, are not essential structures is proved by the fact that they are wanting in many of the Mammalia as well as in Man. They have been observed chiefly in the Rodentia and Ruminantia, where their form and number are subject to considerable variation. The subjoined figure exhibits the ovum

Fig. 376.



Ovum of rabbit surrounded by the tunica granulosa and portions of retinacula. (*After Coste.*)

surrounded by the layer of granules which constitutes the *tunica granulosa*, and externally to this the radiating bands or *retinacula*, the whole of those parts, external to the ovum, being composed of nucleated cells.

Besides these structures, the Graafian follicle contains a pellucid albuminous fluid, of a slightly yellowish colour, partially coagulable by heat. In this fluid float numerous granules similar to those of which the parts just described are formed, together with a varying quantity of oil-like globules.

Lastly, in the midst of the granules at an early period, and subsequently in that more definite arrangement of them which constitutes the *tunica granulosa*, is contained the ovum (*fig.* 374. *f*, and *fig.* 376.), a full description of which is given in the article under that title.

4. *Vessels and Nerves.*—The ovary derives its supply of blood chiefly from the ovarian (spermatic), but in part also from the uterine arteries. So free, indeed, is the communication between these vessels, that the organ may be equally well injected from either source. The communication is effected chiefly by means of a branch of the ovarian artery, which passes inwards to inosculate with a terminal branch of the uterine artery, this anastomotic branch being occasionally so large as to constitute the principal source of supply of the ovary. The terminal vessels are conducted to the lower border of the ovary between the folds of the posterior duplicature of the broad ligament, where they lie in parallel lines, and are readily distinguished by their tortuous or spiral form. Having entered the base of the organ, they spread out into those numerous ramifications which penetrate every part of the ovarian stroma, and give to this structure its peculiar fibrous aspect. From their extreme branches the blood is returned by the veins, which pass to the base of the organ, where they are very numerous (*fig.* 370. *h*). They form, near the ovary and between the folds of the broad ligament, a plexus termed the ovarian or pampiniform plexus, (*fig.* 369. *d*) the vessels of which communicate also with the uterine plexus. Valves are found in the ovarian veins only in exceptional cases.

The ovary derives its nerves from the renal and inferior aortic plexuses.* The nerves enter the organ along with the blood-vessels.

Functions of the Ovary.

The ovary is to the female what the testis is to the male—the germ-preparing organ, the part in which is formed the female generative element, and therefore the essential portion of the entire sexual apparatus. To it all other structures may be regarded as accessory or superadded; for in by far the largest proportion of the animal kingdom they are either found in a rudimentary state, or else have no existence. But not only is the ovary the organ in which the formation and evolution of the germ take place; its offices farther extend to the separation and expulsion of the ova, when they have reached such a state of maturity as will render them susceptible of impregnation. This process, commonly termed ovulation, takes place spontaneously, and without the intervention of the male, which is not necessary thereto. All animals possessing an ovary are subject to this law; and Man constitutes no exception to the rule. But the functions of the ovary are exercised only during a certain period of life. The ova, which are formed at or near the time of birth, and sometimes before that event, are not called into activity until the body of the parent is sufficiently developed, to suffer the parturient act without destruction or serious detriment to its own tissues, such as would be incompatible with the continuance of its own life, and such as is witnessed in those lower tribes where the whole of the vital energies of the parent are exhausted by one effort of reproduction, or its tissues are even disrupted by the process which produces its kind. But long before the time arrives at which the generative faculty is capable of being fully exercised, it is probable that many of the ova which were first formed have perished, their place being continually supplied by new formations.† Their numbers, however, are so great that, if only the one thousandth part of those originally contained

* Snow Beck, Phil. Trans. 1846, part ii.

† Barry, Phil. Trans. 1838, part ii. p. 319. Dr. Ritchie, Med. Gaz., vols. xxxiii., xxxiv.

in the ovary remain, and no new ones are superadded, there will still be more than sufficient for all the purposes of reproduction. But as the functional activity of the ovary, so far as relates to the emission of ova in a state fit for impregnation, is restrained on the one side until the arrival of a certain stage of development of the parent, so on the other a period equally arrives, after which this power of producing and emitting ova altogether fails; and it is plain that both these restrictions contribute to one and the same end, the limitation, namely, of the office of reproduction to that period of life in which the vital energies of the producing body, having attained to full perfection, remain still unimpaired, so that the qualities of health and vigour in the parent may be transmitted undiminished to the offspring.

From this it results that the ovary in Man, as well as in the Mammalia generally, has three noticeable periods: the first, of preparation; the second, of activity; and the third, of decay: and these correspond respectively with the periods of infancy and childhood, of youth and prime, and of decline and old age.

The condition of the ovary at each of these epochs will be traced; but the middle period is obviously that to which the chief interest attaches.

During certain portions of this epoch, and in some instances through more or less of its whole extent, the ovary is employed in ripening and emitting ova. In this respect, however, greater variation is perceptible in different species than in any other particular. But in all alike this one circumstance is observable, namely, that the emission of ova is a periodic occurrence.

Now the periods of emission of ova may so occur as to make the times of parturition coincident with the returns of those seasons which are most favourable for the rearing of the young. In such cases the capacity for impregnation may be limited to one period of the year, the ova being ripened and emitted only at that time. The roe affords an interesting example of this. The doubts which have been sometimes entertained as to the precise time at which the roe becomes impregnated have now been settled by the recent very careful researches of Bischoff*, who has proved that this occurs at the end of July and during the month of August, and that it is only then that the ovaries of the female contain ripe ova, and the testes of the male ripe semen. At other times these are not to be found; hence it follows that in this animal impregnation is impossible at all other seasons.

But in many animals the periods of ripening and discharge of the ova recur with much greater frequency; and probably climate, food, domestic care and the like, exercise a certain degree of influence in modifying the returns of these periods.

In the human female the same periodicity is observable; and it is now rendered in the highest degree probable that in her case the times of ripening and generally of the discharge of the ova are coincident with the times of menstruation*, just as it has been proved beyond dispute that in other Mammalia the same process accompanies that more obvious condition of aptitude and desire for sexual intercourse to which the terms œstrus and rut are applied.

* Entwick. des Rehes, 1854.

A periodical maturation, therefore, of ova, accompanied by dehiscence of the ovicapsules and discharge of their contents, may be said to constitute the principal offices of the ovary during the prime of life. But notwithstanding that these processes are periodically performed, the ovary cannot at any time be said to be in a condition of perfect rest, except under circumstances which will be presently noted; for whilst some ovisacs may be observed to be advancing and preparing to emit ova, others may be seen receding or becoming obliterated. The climax, however, of each serial process is the dehiscence or rupture of one or more follicles. Upon this the whole force of the ovary is, as it were, for the time concentrated. This event being terminated, the activity of the ovary passes away as regards that particular follicle. Enough, however, of vital energy remains in the now useless part to suffice for the healing of the wound, and the closing and obliteration of the cavity left after the escape of the ovum. But the blood gradually deserts the walls of the previously congested ovisac, the distended vessels in its neighbourhood shrink and become obliterated, and the action is transferred to another set of follicles, one or more of which pass through a similar order of changes.

Two circumstances, however, arrest for a time this process. The one is the occurrence of utero-gestation, the other the performance of lactation; and although occasional exceptions may be observed, yet so far as this question has been examined, the evidence collected favours the belief, that in pregnant women and in those who suckle, no ova are emitted during the continuance of either of these processes.†

This view also, so far as relates to lactation, receives support from the well-known circumstance that a considerable degree of immunity from impregnation occurs during the continuance of lactation, a circumstance easily explained upon the supposition that at that time usually no ova are matured or emitted.

It will now be necessary to trace in detail the process of ovulation, so far as regards the structures concerned in that process which properly belong to the ovary.

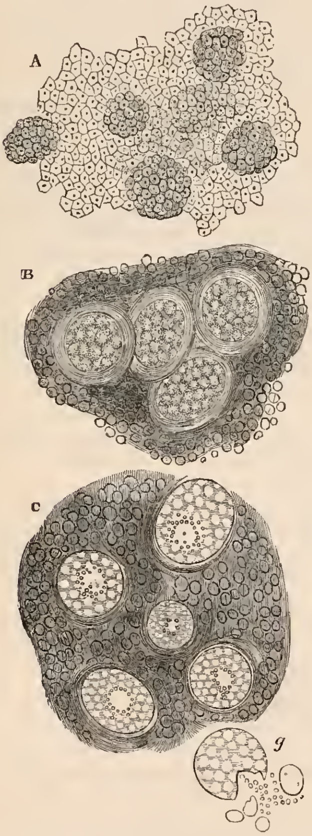
A general account of the Graafian follicle in its mature state having been already given at p. 550., the changes which this important structure undergoes at different periods of its development and decay will now be examined.

* The question of the connection between menstruation and the maturation and discharge of ova from the ovary, is considered under the head "Menstruation" at page 666.

† Négrier, Recherches sur les Ovaires, chap. ii. iii.

First Stage. Origin of the Graafian Follicle.—The time of the first appearance of the follicle within the ovary is subject to considerable variation in the different orders of Mammalia. In all it occurs at a much later period than the first appearance of the seminiferous tubes in the male. Bischoff, who has devoted much attention to the examination of the follicle in its earliest stages of formation, has never been able to discover the least trace of it in the dog and rabbit before birth. This is also the case in most instances in the human embryo, although examples occur of the ovarian follicles being already formed in the new-born

Fig. 377.



Represents the mode of formation of the Graafian follicle. (*After Bischoff.*)

A, portion of ovary of a fœtal dog. The Graafian follicles are seen in the first stage of formation, consisting of little groups of primary cells in the midst of a tissue of similar structure.

B, Portion of ovary of a dog four weeks old; a delicate fibrous coat now surrounds the groups of nucleated cells.

C, Portion of ovary of a pig three weeks old. The follicle is here composed of transparent membrane, the outer surface of which, in the larger ones, is become fibrous. Its inner surface is lined by an epithelium of pale cells (membrana granulosa); within this is the germinal vesicle, surrounded by granules resembling yelk granules. These contents are seen dispersed from a ruptured follicle at *g*.

infant, and in advanced embryos. At first nothing is distinguishable in the ovary except a uniform mass of primary cells and cell nuclei. When the follicle or ovisac is about to form, there may be perceived little round or ovoidal aggregations of primary cells, forming groups which are distributed in considerable numbers through the ovary. These, from the circumstance that the substance of the ovary is likewise composed of similar cells, are scarcely distinguishable from the stroma in the midst of which they arise (*fig.* 377. A).

Now Barry, who also very carefully examined the early formation of the follicle in the rabbit, maintains that within these little groups of cells the germinal vesicle is already contained. Barry represents the germinal vesicle at its first formation as surrounded by minute oil globules, and a collection of granules, forming together little elliptic masses which are distributed through the ovary. A comparison of the descriptions and illustrations of these two observers leaves no doubt that both refer to precisely the same object.

Round these little groups of cells is now perceived a delicate transparent membrane, which is at first apparently destitute of organisation. This is the ovisac in its first stage of formation (*fig.* 377. B, C). The precise mode of its development has given rise to much speculation, which is interesting chiefly with reference to the question whether the ovisac is to be regarded as the vesicle of evolution of the ovum, or whether the ovum, or parts of it at least, are previously formed, and the ovisac is afterwards superadded.

Bischoff explains the formation of the fine homogeneous membrane which is first seen surrounding the little groups of cells by supposing that those which form the peripheral layer become confluent, and that by their junction they constitute this boundary wall, whilst the original cell contents are dispersed.

This membrane soon afterwards becomes lined with a stratum of endogenous cells, which form an epithelium upon its inner surface. A close examination shows further that this cell layer is bounded by a homogeneous tunica propria.

Hence Bischoff concludes that the follicle is, as Henle asserts, a primary secreting follicle, which, like all secreting follicles, is not composed of a primary cell membrane, but results from a confluence of cells. He has never seen in it, when still in the condition of a homogeneous transparent membrane, a cell nucleus, as would be the case in a primary cell. The contents of the vesicle, according to Bischoff, consist of a clear fluid containing cell nuclei and granules; the latter closely resembling the subsequently-formed yelk granules. Somewhat later is observed within these follicle vesicles, which in the meantime have become more developed and numerous, a second transparent spherical vesicle, containing a nucleus which closely resembles, and is considered by Bischoff to be the germinal vesicle. Hence, whilst the observations of Barry, confirmatory of the views of Baer, and supported now by Dr. Allen Thomson*, led the former to conclude that the formation of the ovum commences before the existence of the ovisac, the researches of Bischoff point, on the other hand, to the ovisac itself, as the formative organ of the ovum.

The general appearance of the ovisac, when first formed, is that of a pellucid, and often yellowish vesicle, having an elliptic form, and at first so minute as not to exceed $\frac{1}{50}$—$\frac{1}{100}'''$ in diameter; as, for example, in the ox, the ovary of which animal, according to Barry, would contain in a cubic inch 200,000,000 of such ovisacs.

The ovisac is more or less pellucid, according to its size. In the smaller ones, the walls are so transparent as to admit of the form of their granular contents being seen through them (*fig.* 377. B, C); but as development advances, they become merely translucent. The walls, which are relatively very thick in the small ovisacs, are elastic and distensible, and have an undulating surface, presenting numerous depressions, to which is referable the plaited or folded appearance which the contour of the ovisac assumes under pressure.

The ovisac is sometimes formed in the parietes of an already developed Graafian follicle; but whether originating here, or, as is more commonly the case, in the proper substance of the ovary, it is always at first seen lying perfectly loose in a little cavity, excavated, as it were, in the substance of the surrounding tissues. Subsequently a covering, or tunic, consisting of a rather dense connective tissue, susceptible of becoming highly vascular, and closely connected with the ovarian stroma, is gradually formed upon the outer surface of the ovisac, with which this outer covering now becomes closely united. This is the structure termed by Barry the tunic of the ovisac (*Tunica S. theca folliculi*). And it is by the union of these two that, according to his observations, the Graafian vesicle is formed. At this stage of its development there exist all the elements of the completely-developed follicle, viz., the outer vascular or fibrous coat, the inner softer layer, or proper tunic of the ovisac, and the still more internal epithelial layer of granules representing the membrana granulosa, together with the elements, at least, of the ovum, and the fluid contents of the sac.

These constitute the most important points regarding the development of the Graafian follicle at the time of its first formation in the Mammalia generally. They serve to facilitate greatly the study of the same parts in Man.

With regard to the human follicle, the corresponding stage is most readily observed in the infant, a few months after birth. If at that age a section be made of the ovary, it will be seen to be composed of a parenchyma, which is somewhat lax towards the centre and base, but more dense in the peripheral portion of the organ. The more lax central portion consists of blood-vessels and wavy bundles of connective tissue, the latter being much more distinct in the ovary of the infant than in the adult. The more dense peripheral portion is that in which alone the ova are found. It is made up almost entirely of a mass of minute ovisacs, already containing ova (*fig.* 373.).

These ovisacs, at present in a rudimental condition, are of various dimensions. In the example given, their average diameter was $\frac{1}{500}$—$\frac{1}{1000}''$. But it happens, occasionally, that ovaries of a very early age are found to contain ovisacs or Graafian follicles of comparatively large size. Thus, in a specimen in my possession from a child of seven months, one ovary contains a follicle of rather more than $1'''$ in diameter, whilst the other is almost entirely occupied by five follicles, the largest of which measures $2\frac{1}{2}+1\frac{1}{2}'''$, and the smallest is one quarter of that size. In this case the entire length of the ovary is only $7'''$.

Second Stage. Growth, Maturation, and Preparation for Dehiscence of the Follicle.—When the period approaches, or has already arrived, at which an animal becomes apt for reproduction, and is ready to receive the male, a certain number of follicles progressively increase in size, and become more and more superficially placed. Shortly, the more advanced series occupy the surface of the ovary, and present the appearance of round grains close-set, so as to give to the organ sometimes the appearance of a bunch of grapes (*fig.* 378.). This is more particularly the case in the sow, which affords an excellent example for tracing these changes in the follicle.

Fig. 378.

Portion of ovary of the sow. The Graafian follicles project above the surface of the ovary. Several, riper than the rest, are conspicuous by their size. a, unripe; b, riper follicles; c, stroma.
(*After Pouchet.*)

Each grain, *a*, consists of a vesicle filled with a limpid fluid, albuminous, viscid to the touch, of a slightly yellow colour, and coagulable by heat and alcohol. Their walls, previously diaphanous, now become opaque from the thickening of the *inner* membrane of the vesicle, *i.e.*, of the ovisac itself. From four to six of these vesicles will be found to become simultaneously developed in each ovary (*fig.* 378. *b*, *b*). These are always the most superficial. Their form is generally ovoid. They increase until they attain a diameter of about $\frac{4}{5}''$.

* Page 76. of this vol., Supplement.

The augmentation in bulk of the follicle is, in the first instance, due almost entirely to an increase in its fluid contents. It is probable that this fluid is supplied by the minute capillaries with which the ovisac is furnished, and which, long before the vesicle has attained its full diameter, appear in the form of a rich network upon its inner surface, giving to the latter a bright red colour.

And now a thickening of the walls of the follicle becomes very manifest, accompanied by an exudation of blood which collects in the interior of the sac. The period at which this escape of blood commences is variable. Sometimes it may be seen in follicles of not more than $1\frac{1}{2}'''$ diameter, but more frequently when they have attained a size of about $3'''$.

As this exudation of blood takes place at a period certainly antecedent to the rupture of the follicle, it cannot be traced to vessels lacerated during that process, but must proceed from the congested capillaries just described. It resembles arterial blood, and is rich in globules, which at first remain free and distinct; but when the distension of the follicle has become considerable, the blood coagulates into a dark-red clot.

This pouring-out of blood has been termed the menstruation of the follicle; but beyond the purpose of increasing the distension of the latter, preparatory to its rupture, no use has been assigned to it, except by Pouchet, who maintains that in the sow the ovum lies at the bottom of the follicle, instead of near its upper or free surface; and that as the sanguineous exudation increases, it collects between the inner surface of the ovisac and the membrana granulosa, and so carries upwards the latter, together with the ovum which is lodged upon it. He asserts, further, that in proportion as this exudation increases, the albuminous fluid previously occupying the follicle is absorbed, until the entire cavity becomes filled with blood.

The result of this process is, that the ovum, previously lying at the bottom, is now transported to the upper part of the follicle, immediately beneath the point at which the rupture of the walls is about to take place.

Notwithstanding the minuteness of Pouchet's description, its accuracy, so far at least as concerns the supposed purpose of this exudation of blood, has been called in question. The fact, however, cannot be disputed, that, in many animals, as well as in man, the follicle does contain blood, often in considerable quantity, previous to its rupture. And this is a very important point, because it serves to refute the statement of some who maintain that the presence of blood, or of a clot, within the follicle, affords certain evidence that the rupture of the latter, together probably with the escape of the ovum, has already occurred. Barry also, in his researches upon the rabbit, says, that after certain of the ovisacs have discharged their ova, "some of the larger Graafian vesicles, remaining unbroken, are frequently found to contain a considerable quantity of blood. Such spots, he observes, have been noticed by several observers, who supposed them to indicate the Graafian vesicles from which ova were destined to be expelled.

Thus Barry's prior testimony serves to confirm that of Pouchet and others, to the effect that the blood found within the follicle does not result from its rupture, but that it is there antecedent to that process.

Some other changes which occur in the follicle previous to its rupture may here be noticed. The thickening just spoken of takes place in the inner membrane, or that which constituted originally the ovisac. This thickening is sometimes so considerable as to increase the diameter of the follicular walls to three times their original amount. At the same time, their contour becomes somewhat undulating, and their colour approximates to that of the buffy coat of the blood.

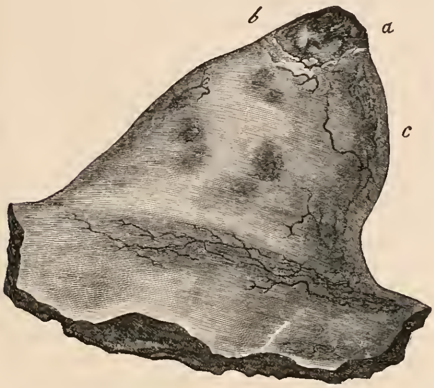
While these changes are going on in the substances and in the contents of the follicle, preparation is being made externally for the rupture at a certain part of the parietes. The base of the follicle continues to be imbedded in the substance of the ovary (*fig.* 379.), but the upper portion projects free above this, being covered only by the usual ovarian investments. Here, at the more salient portion of the projecting vesicle (*fig.* 379.), an increased vascularity is observable. The peritoneum and sublying tissues become exceedingly red, and an abundance of blood is observed in the numerous capillaries which are now visible upon the summit of the vesicle. After this, the fibres of the ovarian coverings become gradually separated, preparatory to their complete laceration. The tunics also of the follicle itself become perceptibly thinner at this spot, which corresponds with the situation of the ovum — always, at this period, lying immediately beneath it.

Fig. 379.

Portion of ovary of the sow. The follicles are in a more advanced stage than in fig. 378. Two of these are preparing for rupture. Already a small aperture is perceptible in the centre, immediately above the spot where the ovum lies; and towards this point the bloodvessels converge. (After Pouchet.)

The same regular sequence of changes, which may always be traced in the Mammalia, though with some slight variations according to species, occurs also in man. If the examination be made in a young and previously healthy woman, who has menstruated regularly up to the time of her death, there will generally be found in the ovary one or more follicles in conditions similar to those just described. The ordinary state in which the Graafian follicle is found has been explained at p. 550. Vesicles in the state there described may be seen at all times in the healthy ovary, sometimes near its surface, and at others buried more deeply; but when they increase in growth beyond this size, and are preparing to rupture, one or more will always be found approaching the periphery of the ovary, or rising above the level of its outer tunics, constituting there a nipple-like prominence, so distinct as at once to arrest attention, and to point out the part of the ovary in which the dehiscence will next occur (*fig.* 380. *a*).

Fig. 380.



Ovary from a woman aged 22, *who died on the tenth day after the commencement of her last menstrual period.* (*Ad Nat.*)

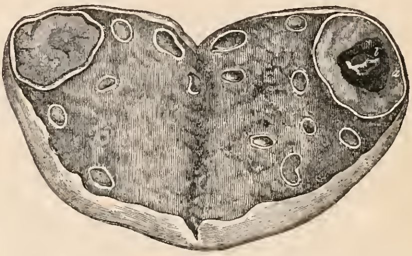
A follicle is preparing for spontaneous rupture at *a*, where a considerable prominence occurs, and where the peritoneal and albugineous coats are almost entirely absorbed.

In general, only one follicle will be found preparing for rupture; but sometimes two, or possibly three, may be observed in the same condition in one ovary. The growth has now been so considerable, that instead of measuring only $1\frac{1}{2}'''$—$2\frac{1}{2}'''$, or even $3'''$, it has now a diameter of $5\frac{1}{2}$—$7'''$, the breadth being usually somewhat less than the length, for it rarely happens that the follicle is perfectly spherical. In consequence of this increased growth the follicle projects from the surface, and causes the swelling just described, whilst the accumulation of fluid within it produces a softness and sense of fluctuation in this part of the ovary, which is very obvious to the touch. Over the centre of this projection the peritoneum is exceedingly thin, and in some places is wanting, partly from absorption, and partly from laceration, the result of overstretching and distension.

The tunica albuginea also of the ovary may be absorbed, or may have become so exceedingly thin, as to permit the blood-coloured contents of the vesicle partially to appear through it, giving to the spot a peculiar brick-red colour. Around the margin or base of the prominence the fibres of the tunica albuginea are often seen to be separated at short distances, forming concentric lines or interrupted circles; the red contents showing through the interspaces, and producing an appearance of alternate white and red lines (*fig.* 380. *b*). Beyond this circumference, the base of the prominence exhibits the usual white colour of the ovarian coverings. Numerous red vessels, chiefly veins (*fig.* 380. *c*), ramify towards the projecting spot, and some of these traverse it to its summit, coursing over the prominence in serpentine lines, and forming here a rich plexus.

A clean section through the centre of the projecting follicle lays open an ovoid cavity,

Fig. 381.



The same ovary (*ad Nat.*) *as in fig.* 380. *laid open, displaying,*

a, the cavity of the enlarged follicle; *c*, the corresponding half of the same; *b*, a blood-clot. Numerous follicles of the ordinary size are seen scattered through the ovary.

(*fig.* 381. *a*), containing usually a deep red clot, *b*, together with a certain quantity of blood and a bloody fluid. The clot has as yet no adhesion to the walls of the cavity, and is easily washed away.

If the ovary has been examined not too long after death, the ovum may possibly be found lying imbedded in the granules of the *membrana granulosa*, immediately beneath the most projecting point of the follicle. But more commonly, the examination not being made until after this delicate membrane has melted down, and its granules have become dispersed by post-mortem change, the ovum cannot be discovered.

After washing out the contents of the follicle, the inner surface of the ovisac is exposed (*fig.* 381. *c*). This I have occasionally seen to be of an intense red colour, from the surface being covered by a rich network of capillaries filled with blood. But most commonly the colour of the ovisac throughout, as far as the outer tissue of the follicle, is at this time a clear, pale, chrome yellow, this coat being now also very soft in texture. It is important to observe that the yellow colour includes the whole thickness of the ovisac, or inner coat of the Graafian follicle, which now measures from $\frac{1}{2}$ to $1'''$ in thickness, but that it extends no further; the outer coat, or theca folliculi, retaining its ordinary condition. Already a slightly wavy outline is perceptible in the follicle (*fig.* 381.), which is due to the growth of the inner membrane having continued after the outer coat has ceased to expand.

The inner coat of the follicle, when it has thus acquired a yellow colour, is seen, by the aid of the microscope, to have undergone an important and yet very simple change. On its inner surface, or that which is turned towards the cavity of the ovisac, it presents the appearance of a transparent and nearly structureless membrane, in the substance of which are imbedded numerous oil droplets, very minute, and aggregated in little masses,

Fig. 382.

Cells filled with oil-granules which give the yellow colour to the inner coat of the Graafian follicle before it has burst, forming the substance termed corpus luteum. (*Ad Nat.* × 350.)

a, separate cells; *b*, the same imbedded in the structureless membrane. (From the same subject as *figs.* 380. and 381.)

with a certain regularity which suggests the idea that they have either been originally deposited around a centre globule, or are contained in cells or vesicles, the cell-wall of which is not very discernible (*fig.* 382. *b*). Deeper towards the outer surface of the ovisac the oil droplets or granules become so numerous as to prevent the recognition of any other structure until the greater portion of the oil has been dissolved out by macerating the part in ether. If, after this process, the tissue which remains be washed in spirit or water, and subsequently treated by acetic acid, it is seen to be composed of numerous blood-vessels, and of developed as well as embryonic fibres of connective tissue, which latter, however, are only faintly indicated, and are connected together by a transparent membrane. The proportion of developed fibres of connective tissue is here very large, whilst in less advanced follicles the embryonic fibres preponderate (*fig.* 375.).

Another and perhaps more satisfactory mode of examining the yellow coat of the Graafian follicle in this stage, consists in slow maceration in a very weak preservative fluid (glycerine and water). The cells, which this coat contains in great abundance, can now be obtained separately for observation. They are seen to consist of a transparent cell-wall, filled with oil granules (*fig.* 382. *a*). The average cells vary in diameter from $\frac{1}{800}''$ to $\frac{1}{2000}''$, but many are smaller, and others larger. Occasionally a cell may be seen to have burst, its contents having escaped; a few oil granules, however, may still be perceived adhering to the cell-wall, the torn margins of which are very readily defined. There can be no doubt that these cells are the "peculiar granules" so frequently described and figured by Barry in his account of the various conditions and stages of development of the ovisac.

The colour of the yellow coat—the so-called *corpus luteum*—is not alike in all animals. In some of the Mammalia it is of a bright orange; in others it inclines to red. In Man, as already stated, the inner surface of the follicle, when ripe, is occasionally so loaded with bright red capillaries that the usual appearance is obscured, but its ordinary aspect presents the clear chrome yellow just described. That this yellow colour, like that of the yolk of the bird's egg, is due to the presence of the oil globules (*fig.* 382. *b*) which everywhere penetrate the tissues of this coat, is rendered sufficiently apparent: first, by the fact that treatment by ether, which dissolves out the oil granules, leaves the remaining membrane nearly white; and secondly, that maceration in water has, to a certain extent, the like effect, but in this case arising from the maceration, causing the animal membrane to swell and become opaque, thus obscuring its previous transparency, and rendering the oily portions only faintly discernible through it, as judged by the naked eye, though they are still readily discoverable under the microscope.

Third Stage. Period of Rupture or Dehiscence of the Follicle, and Escape of the Ovum.—This is termed by Pouchet the period of parturition, in which, after the preparatory changes already described, the ovum quits the Graafian follicle in order to enter the Fallopian tube. It is therefore for the ovisac what the process of parturition is for the uterus, viz., the act by which the ovum, after being matured to a certain point of perfection, is expelled from its cavity.

The process by which the dehiscence of the follicle is effected in Mammalia is in some respects different from that which causes the expulsion of the ovum, from its containing capsule, in the vertebrata below them. In birds, reptiles, and fishes, and, indeed, in the Invertebrata generally, the ovum is of so large a size in comparison with the ovicapsule, that the simple increase of the former, as the time of the ovipont* approaches, is sufficient to cause the bursting of the sac at the point where the coats have been prepared for rupture by previous attenuation. But in the Mammalia the bulk of the ovum bears so small a proportion to its containing follicle, that the ovum itself contributes in no degree to the rupture by which it is enabled to escape. In this process it remains a passive body, at least in a mechanical point of view, though doubtless it is the perfecting of the ovum which gives the vital impetus to that series of changes by which it is finally released from its first abode. But the act of

* I have anglicised the French term *oviponte* (ovipont), to express the escape of the ovum from the ovary; while "ovulation" is employed, in a more general sense, to include also the process of its maturation.

parturition is accomplished by other means. The process by which this is effected has been compared by Blumenbach to the spontaneous bursting of an abscess. Here the process consists in an increasing accumulation of fluid within, conjoined with a gradual attenuation of some particular part of the containing walls. So many points of similarity, indeed, may be traced between these two processes, that the term "inflammation" is employed by some authors in describing the preparatory changes in the Graafian follicle.

The resistance which the ovum and other contents of the vesicle require to overcome before any portion of these can escape consists, it must be remembered, in the combined opposition of no less than four membranes, in addition to any portion of the proper ovarian stroma which may intervene. These are, first, the ovisac; then its capsule, united to the former, and with it constituting the Graafian follicle; thirdly, the tunica albuginea; and fourthly, the peritoneal covering of the ovary. These four, shortly previous to the rupture, become so intimately united together that it is no longer possible to separate, nor is it easy always to distinguish them from each other, with the exception, however, of the innermost layer, which can generally be more easily traced than any of the rest, on account of its peculiar yellow colour.

Upon the surface of the most salient portion of the projecting follicle (*fig.* 380. *a*) the peritoneum, as already stated, may be wanting; the tunica albnginea also beneath has become greatly attenuated, and is sometimes found completely eroded, whilst internally the yellow coat of the follicle is also observed to be thinnest about this spot. Every preparation, therefore, is made for the laceration of the follicle at a given point, the seat of which can also be further determined by the observation that in this place the conjoined membranes, previously highly vascular, have become more transparent, whilst their vessels, having become atrophied by compression, now carry little or no blood.

A very slight force is now sufficient to produce the rupture of the follicle in this precise spot, and such a force is supplied by the gradual accumulation of fluid, whether albuminous or sanguineous, or both, within the cavity.

It is believed by Coste that when the ovisacs have reached this point, which is the full term of their growth, they may remain stationary until a state of excitement arises, produced partly by the maturity of the ovum, and partly by the approach of the sexes, and that it is under the influence of such an excitement that the rupture of the follicle most commonly takes place. What probability there is for such a supposition will be hereafter more fully considered. Whether influenced by any external stimulus, or whether occurring spontaneously, and from causes existing within the follicle, the increase of its fluid contents becomes at length so great that the cavity is distended beyond measure, and its walls can no longer resist the pressure, but give way at the thinnest and most projecting part. But it is probable that another power comes also into operation to aid this process. The wavy outline which has been already noticed (*fig.* 381. *c*) as presented in a slight degree by the still unbroken ovisac, together with a certain amount of thickening of this coat, indicates a growth of this more rapid in proportion than that of the outer layer or tunic of the ovisac. This, therefore, will in some degree add to the pressure, because the outer layer of the follicle not being distensible beyond a certain limit, any increase of the contents, whether fluid or solid, will alike contribute to augment the force which is brought to bear upon the weakest point of the walls.

As soon as the rupture has taken place, and the opening in the coats of the follicle and in the corresponding portion of the ovarian coverings is sufficiently large to admit of the passage of the ovum, the latter escapes, together with portions of the membrana granulosa.

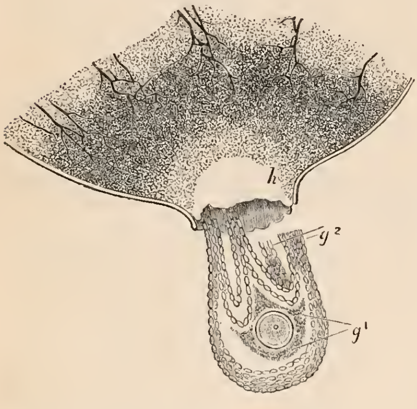
On one occasion Pouchet was so fortunate as to meet with an opportunity of observing the ovum as it was in the act of escaping from the ovisac, and was lying between the margins of the lacerated opening.

Of the five coats which together compose the ovarian and follicular walls, four only, it will be observed, can offer any obstacle to the escape of the ovum; because the membrana granulosa, which is the innermost of all, contains rather than covers the ovum, whose escape cannot be impeded, but will be rather assisted by that membrane. Barry explains the mode in which this probably occurs as follows: — The ovum, imbedded in the cumulus and granular disc which form the centre of the membrana granulosa, at the moment when the laceration occurs, experiences the *vis à tergo* occasioned by the pressure forward of the fluid, endeavouring to escape from within the follicle. This pressure is increased by the thickening of the inner wall of the follicle, amounting in some instances to an exuberant growth, which will act upon the ovum through the medium of this fluid. The obstacle to the escape of the ovum which had up to this moment existed, being removed by the laceration and absorption of the ovarian and follicular walls, that portion of the membrana granulosa which lies immediately behind the lacerated coats, where the ovum is imbedded, presents a surface for the operation of the *vis à tergo* more or less considerable, according to the extent of the rupture.

And now the elasticity of the coats of the follicle, together with some pressure from the weight of the parts surrounding its base, come in aid of this force, and complete the expulsion of the ovum, which escapes together with a portion of the membrana granulosa, and passes into the infundibular end of the oviduct.

Fig. 383. shows the mode in which this process occurs in the rabbit. Here is represented a portion of a ripe Graafian vesicle, which was upon the point of discharging an ovum. The follicle, after being dissected out of the ovary, has been subjected to slight lateral pressure in the compressorium, by which the follicle has been burst at the point (*h*) preparing for rupture. The ovisac has given way at the thinnest point, and the ovum, surrounded by the *tunica granulosa* (*g*, 1.), and dragging after it portions of the *retinacula* (*g*, 2.) is shown in the act of escaping from the follicle.

Fig. 383.

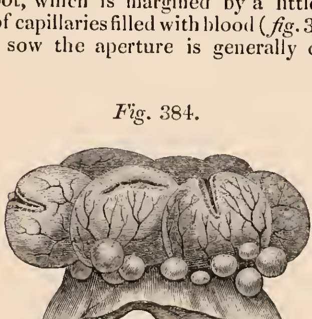


Ovum of the rabbit in the act of escaping from a ruptured Graafian follicle. (*After Barry.*)

The ovum is surrounded by the tunica granulosa, g^1, and draws after it the portion of membrana granulosa termed the retinacula, g^2; at *h*, where the rupture has taken place, the coats of the follicle are attenuated, and towards this spot numerous vessels converge.

The form and size of the aperture by which the ovum escapes varies considerably. In the rabbit it generally appears in the form of a small round aperture in the midst of a bright red spot, which is margined by a little network of capillaries filled with blood (*fig.* 383. *h*). In the sow the aperture is generally oblong

Fig. 384.



Portion of ovary of the sow. Three of the largest follicles have burst simultaneously, and exhibit wide lacerations. Others, less forward, remain unruptured. At the base are several unripe follicles. (*After Pouchet.*)

(*fig.* 384.), and from 1½ to 7‴ in length; the laceration in the latter sometimes extending through the entire diameter of the follicle, and permitting the escape of the whole of its contents, together with the ovum.

The laceration is not necessarily limited to a single follicle. In multiparient animals (*fig.* 384.) all or a greater portion of those follicles which have attained their full development undergo laceration, and emit their ova about the same time. In some of these, however, the effort may prove abortive, and the follicles may remain stationary until another impulse to rupture occurs, and the ova may then be discharged, or may, on the other hand, perish or be absorbed.

In Man, although generally uniparient, two or more follicles may likewise become matured about the same time, and their bursting may take place simultaneously. Of this fact I possess the proof in a case (*fig.* 409. page 605.) in which I found in one ovary three distinct apertures leading to as many developed ovisacs, all of which presented the characters just described as indicating the recently ruptured follicle. In this case the woman died during menstruation.

Such an observation is interesting, as showing in what way multiple pregnancies may occur in the human subject, for the whole of the ova discharged under such circumstances may be impregnated by a single coitus; although it is also possible that the bursting of one follicle only may suffice for the production of twins, since two ova have been several times observed in a single follicle in the Mammalia, and this may also possibly be sometimes the case in Man.

Before proceeding to the consideration of the remaining changes which the Graafian follicle undergoes, it may be useful here to make one or two observations on the conditions already described. Up to the moment of rupture, the progress of the follicle is one of regular advancement from an embryonic condition to a state of full maturity. The object of this progressive advancement is the protection, maturation, and final expulsion of the ovum, in such a manner that this last step may occur at a time when the ovum will be placed in circumstances the most favourable for impregnation.

In order to accomplish this, the ultimate purpose of all these progressive changes, the ovisacs which had been previously set more or less deeply in the ovarian parenchyma reach, one by one, the surface of this organ, and there, swelling rapidly from the increased secretion into their interior, and the growth of their walls, as we have seen, burst and emit their contents. The whole of these changes occur in regular sequence, and affect one or more follicles in succession. These follicles, lying buried in countless numbers in the substance of the ovary, supply, as it were, the pabulum for the morphological changes here described; a certain number only being called into full maturity, whilst the greater portion of those which were originally formed in infancy, or which may continue to form during life, undoubtedly perish. No sexual influence is needful to the production of any of these changes. The whole occur spontaneously, whatever may be the condition of the female.

How far the influence of the male may assist in hurrying on to maturity any of these processes is a question which will be considered hereafter, when the proofs of the statements now made as to the independence of these processes will also be investigated. But it is sufficient here to refer to the fact of the spontaneity of these occurrences, in order to place under one category all the changes which the ovary suffers, up to a certain point, independently of any sexual influence.

Two circumstances here also may be more especially noticed: the one is, that the yellow colour which the proper ovisac or inner coat of the follicle exhibits towards the term of its ripening is distinctly recognisable for some time anterior to the occurrence of the rupture. It occurs in all follicles at this stage alike, both in Man and animals, and under all circumstances, whether coitus be permitted or not; but even when coitus is permitted, it is found at a period long anterior to that at which the act of coition could by any possibility be influential in its production.

The other circumstance which it may be important here to notice is, that the yellow structure is no new nor superadded part, but is the ovisac itself, altered by the gradual deposit in its texture of a yellow oil, which at length accumulates to such a degree as to convert this previously translucent wall of the follicle into an opaque yellow membrane or coat. But neither in any of these stages, nor in any subsequent ones, is there interposed either between the walls of the follicle or between these latter and the surrounding ovarian stroma, any new substance or body of any kind. The yellow colour is confined to the inner coat of the follicle, nor have I ever seen it in any one instance penetrating to the outer coat or covering of the ovisac. There is only one new coat formed, which will be hereafter described; and that coat, often of considerable thickness, is a part entirely superadded, which, after a certain stage in the metamorphosis of the follicle, is applied in the inner side again of the yellow coat, to which it forms a lining. This, although a new formation, is also, as will be presently shown, constructed out of materials existing in the follicle before its rupture.

The final purpose of the Graafian follicle being now accomplished, it may seem a matter of comparatively little interest or importance, in a physiological point of view, to trace its ultimate conditions; for the changes which this structure next undergoes have for their object solely its obliteration. But the process of obliteration or retrogression does not, like the process of development, take place under all circumstances alike. Here the influence of impregnation is exhibited in a degree so remarkable as to have given rise to a general belief that the changes experienced by the follicle, when impregnation has accompanied or followed its rupture, are essentially different in their nature and character from those which ensue when impregnation has not taken place; whereas these differences, it will be shown, are differences chiefly of degree; and yet they are so considerable as to have called forth almost as great a share of attention as has been given, perhaps, to any structure in the human body.

But great as is the interest attached to this structure on account of the evidence which it may afford of the previous occurrence or non-occurrence of impregnation, yet, so various are the views and statements of those who have specially directed their attention to the subject, that neither among physiologists, pathologists, nor medical jurists, can it be said that there is at present any concord of opinion or common ground of understanding.

Admitting, however, for the present that there is a marked difference observable in the changes which the Graafian follicle undergoes, according as impregnation has or has not accompanied or followed the escape of the ovum, we thereby obtain a starting-point, or rather a point of divergence, from which we may follow out these changes in two different series: the one series will include the alterations in the follicle which ensue when impregnation fails, or does not occur; the other, those which it experiences in consequence of impregnation having taken place.

Fourth Stage. Period of Decline and Obliteration of the Graafian Follicles.

A. *Without Impregnation.*—This constitutes the first degree of the descending scale in the history of development of the follicle. Immediately after the escape of the ovum, the inherent contractility of the tunica albuginea of the ovary occasions a diminution in the prominence of the lacerated vesicle. The margins of the opening become approximated in consequence of the collapsing of the walls, and from the edges of the laceration there occurs a slight fibrinous exudation which causes them to become agglutinated. If the aperture has been of considerable size, and no clot remains in the cavity to keep its walls from collapsing, the process of obliteration may proceed rapidly; but if a clot remains, and especially if it is of considerable size, it will serve to support the walls, and prevent them from quickly shrinking.

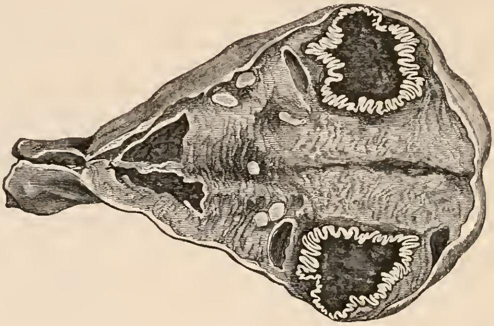
These different conditions will for a time affect the new disposition which the inner membrane of the follicle takes soon after the rupture is complete. In proportion as the cavity is empty, the elasticity of the outer fibrous coat will, by its retraction, occasion a diminution of the cavity; but the inner coat, having already increased during the growth of the follicle in a greater degree than its outer covering, will now, in this collapsed and nearly empty condition of the sac, suffer the same change that would result from enclosing a large bladder within a smaller one.

The inner coat becomes folded, and forms convolutions, which increase and become deeper in proportion as the retractility of the external tunic increases.

These convolutions in the inner and now yellow coat of the follicle are so distinct and striking (*fig.* 385.) as to have suggested those comparisons with the cerebral convolutions which so many authors have employed in describing this change; for the colour, as well as the nature and arrangement of the foldings, constituting ridges and sulci, produce an exact miniature resemblance to the surface of the brain.

If the blood-clot, which is generally found contained within the ruptured ovisac, be of considerable size, its surface will frequently exhibit little furrows, more or less deep, cor-

Fig. 385.



Section of the ovary of a woman who was poisoned by opium. A large Graafian follicle, which had recently burst and discharged its contents, is laid open. The part of the ovary surrounding the aperture was loaded with vessels full of blood. The convolutions of the collapsing follicle are very distinct. The follicle is empty. (*Ad Nat.*)

responding with the convolutions of the ovisac, by contact with which they have been impressed. This clot becomes adherent to the walls of the ovisac; assumes by degrees a pale rose hue; and gradually diminishing by absorption and contraction, it constitutes a centre, towards which the rays of the convolutions from all sides are directed.

But if there be no considerable clot in the centre of the follicle, then its closure proceeds more rapidly. The angles of the convolutions approach each other more nearly, but there still remains a space in the centre which may be empty, or contains only the debris of old coagula.

Lastly, if the cavity is empty, the retractility of its outer coat soon effects its closure. The angles of the convolutions, now compressed one against the other, come into contact across the cavity, and end by adhering together, and so the cavity is obliterated.

If, during the progress of these changes within the follicle, the external surface of the ovary be examined about the seat of rupture, it will be found that the parts in the immediate neighbourhood of the laceration become paler, that the blood gradually deserts the vessels, which were before highly congested, in this situation; and that, as cicatrisation advances, the zone becomes less and less distinct, disappearing, finally, about the time when the last traces of the laceration are effaced.

These changes in the ovarian follicle after rupture exhibit certain differences among the Mammalia, in some of whom, for example, there may be seen to project from the aperture a fleshy mass, sometimes occasioned by the presence of a coagulum, but more constantly by an exuberant growth of the lining membrane of the follicle, which for some time protrudes through the orifice, and may often, at this stage, be drawn out entire by the forceps, without difficulty. Its colour is not alike in all the Mammalia. In the sow, it resembles the liver of a calf; in the cow and sheep, it is of a brick-red.

In Man, the follicle has generally shrunk to very small dimensions by the time that one or more of the next series, which is preparing for development, have reached and protruded from the surface. The cavity by this time is nearly effaced. The chrome-yellow colour of the walls has also disappeared, and the ovisac has gradually become white. Its appearance upon section at this time is very striking and characteristic. In the centre (*fig.* 372. *h*) is still perceptible a small space, which might contain the head of a pin. It is surrounded by a white irregular circle, from which proceed outwardly about a dozen little rays. The circle is formed by the united inner angles of the follicular convolutions. The rays consist each of a double layer of the folded membrane. The apices of the rays are the original outer angles of the serpentine folds or convolutions of the ovisac. The outer coat of the Graafian follicle can now no longer be seen. At this time, the remnant of the shrunken vesicle measures about $1\frac{1}{2}'''$ diam.

Finally, whilst the foregoing changes are proceeding internally, a corresponding alteration takes place at the surface of the ovary.

The closure of the aperture, by cohesion of its opposite sides, occasions a drawing together of the surrounding parts, and the accompanying collapse of the follicles causes the part of the ovarian surface in this situation to sink inwards. The depression thus caused is increased by the continued shrivelling of the follicle, and by its retiring inwards towards the centre of the ovary. This latter change is occasioned not so much by any activity on the part of the now empty follicle as by the approach of new and rising ones to the surface, by which the empty and useless ovisacs are now pressed aside.

By these successive retirings of the follicles after bursting, and by the cicatrisation of their apertures, the ovarian surface becomes gradually indented in all directions so as to exhibit those pits and furrows which are always seen upon the ovary in advanced life (*fig.* 390.); and these, occurring in women under every circumstance alike, afford one of the most convincing proofs that this discharge of ova from the ovary may and does occur independently of sexual congress.

Finally, the stellate remains of the follicle continue to decrease, and become gradually buried in the ovarian stroma, until they are entirely obliterated, thus giving place to other vesicles which pass through the same stages of growth and decadence.

B. *After Impregnation.*—Very different is the progress of the Graafian follicle after impregnation has taken place. Here, although the changes which occur have no other intelligible purpose than that of the final obliteration of the follicles, yet the process takes place much more slowly than it does when the ovipont has not been followed by conception. In this latter case, the metamorphosis of the follicle into the small yellow stellate organ takes place usually within a month from the time of rupture, and its subsequent reduction to the little white cicatrix previous to its total disappearance is completed in about the like period. But the follicle, which has discharged an ovum that has been afterwards impregnated, is not obliterated in a shorter time usually than 13—14 months. During that time it appears to undergo a great and remarkable development. But a close examination shows that this is not true development, in the ordinary sense of the word. It is not a forward movement, progressing towards any new purpose or end, but is only the same process of obliteration, conducted upon a larger scale, and with a greater abundance of materials than in the case of the ordinary follicles when impregnation has not occurred.

Apparently the chief difficulty which has stood in the way of a clear comprehension of this has arisen from a want of sufficient consideration of those altered circumstances in which the generative organs are placed after conception; for, from the moment that impregnation has occurred, all parts of the generative apparatus are brought under the influence of a common stimulus, and all manifest in a greater or lesser degree some progressive change. This is more particularly observable in the internal organs, and especially in the uterus, which very soon receives a larger supply of blood. But the blood-vessels supplying the uterus inosculate so freely with those of the ovary, that the two organs may be practically regarded as deriving their blood from one common source. Each may be injected from the vessels of the other, and though only one set be selected, both are alike filled.

Hence it may be assumed that, although there is no direct continuity of texture between the ovary and the uterus, yet, under the influence of a common supply of formative material, as well as a common innervation, there may be established such a consent of action as will account, in some degree at least, for the differences which we are now about to consider; for when, after the discharge of the ovum from the ovary, impregnation fails, or has not been attempted, the internal organs, previously highly vascular, subside into a passive or quiescent state until the period of the next ovipont approaches, when the uterus again exhibits the same condition of turgescence. But if impregnation has taken place, then the turgescence of the uterus, far from subsiding, only increases, and certain of its textures now become rapidly evolved. The reproductive act, however, does not commence in the uterus. The ovary is the seat of the first changes, and the uterus is only placed in a condition of readiness, on each occasion of the ovipont, to carry on and complete the process which has been commenced in the former organ. The absence of impregnation, on the one hand, is the cause of the failure of the further stages of the process; the occurrence of impregnation, on the other hand, establishes these stages; consequently the ovisac which is about to discharge, or one which has just discharged an ovum, and the uterus which is about to receive or which has just received that ovum, are both placed under similar conditions. Whatever influences the one in the direction of development, affects the other also, to a certain degree, in the same direction. Whatever, on the other hand, determines the retrogression of the one, determines, in like manner, the receding of the other. If the ovum has become impregnated, the follicle which was the first birthplace of that particular ovum, and the uterus which subsequently receives and protects it, continue alike to suffer change. But if the ovum perishes, the recipient organ feels no stimulus, is not excited to further preparation, subsides into its former state of quiescence, and its producing capsule likewise shrinks, and finally disappears. If the inquiry be prosecuted further in the hope of eliciting some more satisfactory explanation of this remarkable series of changes, the investigation will, in the present state of our knowledge, be found altogether to fail. The question, *Cui bono?* continues unanswered, but the fact remains, and the law appears to be invariable.

When conception has followed the discharge of an ovum from the ovarium, the follicle which produced it closes in the same manner as when conception has not occurred, but it does not shrink rapidly, as in the latter case. On the contrary, the inner coat or original ovisac continues to increase in thickness, in consequence of a still larger deposit of yellow oil granules in its substance. The outer coat of the follicle or tunic of the ovisac suffers no change; but upon the interior of the ovisac, and therefore lining the cavity, is formed a membrane, the origin and nature of which will be presently considered; or else it may happen that the cavity becomes obliterated by the organisation of the clot by which it had been at first filled.

After conception it is probable that the actual diameter of the follicle does not at any time materially increase. So great, however, are the variations in its size in different subjects, that this point scarcely admits of being accurately determined. The Graafian follicle may, at the time of rupture, occupy $\frac{1}{4}$, $\frac{1}{3}$, or $\frac{1}{2}$ of the entire ovary. These at least are the dimensions which it is usually found to have, in different instances, during the first four months of pregnancy; but after this period the process of diminution begins to be perceptible. All the changes which are now observable in regard to form, solidity, and other particulars obvious to the unaided senses, and all the histological changes are to be looked for within the outer coat of the follicle. The latter appears to suffer no alteration, but simply to follow the movements of its contained parts, around which it remains loosely applied. The ovisac, however, or inner coat, rapidly increases in thickness, in consequence of a more considerable accumulation in its texture of the same yellow oil whose deposition had begun in it long before the follicle had ruptured, and when it was only approaching the surface of the ovary.

This thickening of the inner follicular coat is followed by a twofold result. The membrane, being confined by its outer tunic, now no longer distensible, as well as by the surrounding stroma into which the vesicle has now begun to sink, becomes more deeply plicated; and since it can no longer extend outwardly, it must of necessity encroach upon the cavity within. The latter thus becomes sensibly diminished, whilst the entire thickness of its boundary wall is in like proportion increased.

At the end of the first two months of gestation, the follicle possesses considerable solidity. The wavy and plicated condition of the yellow ovisac is now less distinct. The whole of this coat exhibits the appearance of a thick yellow layer, still occasionally traversed by numerous little blood-vessels, which run across it in straight lines from without inwards as far as its inner surface. The larger of these vessels probably do not actually pierce the yellow coat, but lie between the sulci, representing the original folds of the ovisac, and which, now pressed back to back without being yet obliterated, would still serve for the conveyance of blood-vessels to different parts of the tunic.

These changes continued to be in a certain sense progressive until the fourth month of gestation, about which time the Graafian follicle is usually considered to attain its highest state of development. But if the term development be admitted, it should be remembered that the only apparent purpose of these and other changes which ensue is still the obliteration of the structures in which they occur. The process of obliteration, however, has at this time not proceeded so far as to have caused the removal or even diminution of any of the original parts composing the follicle, whilst some new structures are superadded or produced by metamorphosis of the original materials.

The follicle at this period generally affords the best opportunity for observing the changes which result from impregnation. It may therefore be selected for a critical examination of the subject.

The external condition of the ovary in which such a follicle is contained serves at once to point out the precise seat which the structure occupies. Not only is the entire ovary larger than that of the opposite side, but it appears more swollen, and is perceptibly harder in one particular spot; over or near this spot a cicatrix may still be visible, and in its immediate neighbourhood are often found some serpentine vessels. If, now, a section be made of the ovary in this situation so as not to pass through the centre, but to include only a portion of the circumference of the follicle, the latter will present the condition represented in *fig.* 386. The follicle, in the

Fig. 386.

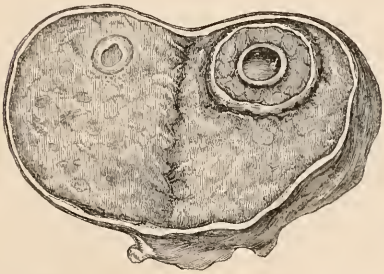
Section of the ovary of a woman who died at the end of the fourth month of utero-gestation. The Graafian follicle of the ovum which had been impregnated projects above the stroma. (*Ad Nat.*)

a, outer vascular coat (tunic of the ovisac); *b*, yellow inner coat (ovisac), from which a thin slice has been removed, not deep enough to lay open the cavity, but displaying the brain-like convolutions; *e*, portion of the follicle corresponding to *b*.

form of a little globe, is seen to occupy about a fourth part of the ovary. Its solidity and spherical form cause it to project considerably above the surface of the section. In this way is exposed the outer coat by which the follicle is bounded. Upon this coat numerous blood-vessels, derived from the ovarian stroma, ramify. It is the tunic of the ovisac, the original outer coat of the Graafian follicle, which in all the transformations of the latter suffers no change, until the time arrives when the whole body finally shrinks and disappears. The position and relations of this coat to surrounding parts leave no room for doubt as to its identity. Nothing bounds it externally but the stroma of the ovary. Nothing lines it internally but the yellow ovisac. Neither between its outer nor its inner surfaces, and the corresponding structures just named, is there at any time found any substance or medium interposed. This coat has undergone no material thickening, and its histological elements are simply those of the outer coat of the follicle, the same as before impregnation has occurred.

Proceeding inwards, the next coat is yellow; it has a nearly uniform thickness of $1\frac{1}{2}'''$. In its substance may still be seen traces of the original foldings or convolutions. These are more easily shown upon the surface of the first section (*fig.* 386.), but are less obvious in one carried deeper so as to include the centre of the follicle, where the

Fig. 387.

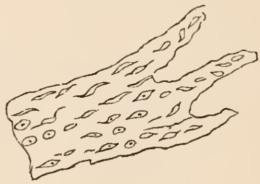


Deeper section of the same Graafian follicle as in fig. 386. *The cavity, which contains a remarkably clear fluid, is exposed.* (*Ad Nat.*)

a, outer vascular coat (tunic of the ovisac); *b*, inner yellow coat, or corpus luteum (ovisac); *c*, white membrane lining the cavity (a new formation); *d*, cavity empty.

coat shows greater solidity (*fig.* 387.). Up to this time, however, and sometimes later, the vessels still traversing this coat in the lines of its former convolutions may be traced in many specimens, and the capillaries may still be filled by a successful injection to such an extent as to render the whole mass crimson.* Examined by the microscope, the following results are obtained:—The yellow coat, $1\text{-}1\frac{1}{2}'''$ thick, is soft, swells in water, and is easily torn into fragments which nevertheless hang together, being connected by a tough flexible medium. During this process numerous oil droplets escape, and form, with the drop of water in which the preparation is placed, a highly refractive fluid. This fluid, when examined, is seen to contain numerous particles of inappreciable size endowed with molecular motion, minute granules, and oil globules, which are at first also very minute, but soon collect and coalesce into larger drops that float to the surface of the fluid. The substance of the preparation also is everywhere pervaded by the oil drops which obscure its structure, and prevent further examination in this state. The preparation, having been treated next by ether, and subsequently washed in alcohol and replaced in water, it is found that the oil has entirely disappeared. The principal portion of the remaining substance has the appearance of a granular membrane, but in many places slightly wavy lines of connective tissue are perceptible. From the margins project in many places flattened bands composed of 8-10 filaments of common connective tissue, united by membrane, and having attached to them numerous granules. Separate fibres also appear at the margin of the preparation, but only from forcible detachment. Treated further by acetic acid, the oil globules, as well as the fibres, have totally disappeared. The course of the latter is now only indicated by numerous lines of round, oval, or elongated nuclei (*fig.* 388.), which are everywhere abundantly seen attached to a fine, structureless, transparent membrane. The outlines of the

Fig. 388.



× 350.

nuclei are very sharp and distinct, and within them are contained one or two nucleoli. This coat is traversed by numerous blood-vessels and capillaries, and to their coats in all probability many of these nuclei belong.

The yellow coat is bounded internally by a third tunic which is white, having precisely the milk-white colour, and very nearly the consistence, of articular cartilage. It is of variable thickness, but often $\frac{2}{5}'''$ or more in diameter. It is very tough and coherent in texture, and is with difficulty split by needles, breaking into irregular fragments. These, examined by the microscope, are seen to be composed of tough fibres of connective tissue, whose arrangement in wavy lines may be perceived through the mass, but which are so closely connected together, by a semitransparent membranous medium as to be inseparable into distinct fibrillæ, except at the margins of the fragments, where they are tolerably distinct; where also the connecting medium may be seen in the form of a structureless membrane. Minute granules are everywhere seen scattered throughout the mass, and adherent to the detached fibrillæ. Treated by acetic acid, the fibres become transparent and pale, their outlines being hardly distinguishable. Oval nuclei, rather scanty, lie in the direction of the fibres. The whole sub-

* Montgomery, Signs of Pregnancy, p. 227.

stance has the appearance of a tissue which is in a low state of vitality.

It is probable that the presence of this coat within the follicle has been the cause of most of the differences of opinion which have existed regarding both the seat and the nature of the yellow portion of the follicle of pregnancy. It seems to have been assumed, without further examination by many who have written upon this subject, that the coat last described is one of the coats originally composing the Graafian follicle; whereas it is formed by the metamorphosis of the blood-clot, already described as occupying the centre of the follicle before even the ovum escapes. I have seen very distinctly the fibrillation of this clot soon after the follicle has closed. It is then found to be gradually becoming pale, the red particles disappear by degrees, the clot adheres firmly to the inner surface of the ovisac, and the mass is converted into the low form of tissue just described, which may either take the condition of a membrane lining the cavity and leaving a central space filled by transparent fluid, or the whole may be converted into a solid body. Either of these forms may be observed, and the knowledge that each may occur disposes of the speculative question as to the time when the cavity of the follicle is obliterated.

On the other hand, the yellow coat which has been often described by authors as altogether a new formation, deposited either between or external to both of the follicular coats, can be most easily traced through all its phases, beginning in the ascending vesicle, as the original ovisac; its structure filled with nucleated cells, which gradually become charged with oil droplets until the whole tissue assumes the peculiar yellow which is so distinct about the time of bursting of the follicle. And this colour it never loses until the time of its complete obliteration approaches; but through all the subsequent changes of the follicle the same anatomical structure and the same relative position of parts is preserved.

In the original preparation from which *fig.* 387. was taken, nothing served to distinguish the several coats better than their colour. The outer coat or theca folliculi was red; the second coat, or ovisac itself, chrome yellow; the now internal and newly formed coat was milk-white.

It remains to describe the cavity in the interior of the follicle, which, though sometimes obliterated, is more frequently found still existing at the fourth month of utero-gestation. In the specimen represented in *fig.* 387. the cavity measured 3‴ in diameter and contained a clear gelatinous fluid. In other cases a cavity at this time no longer exists, but the centre of the ovisac is occupied by a tough white substance, whose origin has just been explained.

It will not be requisite to follow out minutely the remaining changes which the Graafian follicle undergoes. After the fourth or fifth month of pregnancy a certain diminution in size begins to be perceptible. The walls of the cavity approach nearer to each other, and the white lining becomes thinner, and begins to be folded into plaits which, radiating outwardly, are seen intermingling with the yellow colour of the proper ovisac (*fig.* 389.). The outer boundary of the follicle also now presents an irregular and somewhat angular and occasionally an oval outline. These changes proceed with much variation in different subjects; but usually at the time of delivery the ovisac, though still yellow, has lost much of its brightness, and the cavity, if it had existed, is replaced by a solid white stellate cicatrix (*fig.* 389.) caused by the folding of the white lining

Fig. 389.

Graafian follicle two days after mature delivery. The white lining of the cavity (c, fig. 387.) is here folded into a stellate figure. It is surrounded by the darker yellow ovisac (corpus luteum), whose outline is become angular. (After Montgomery.)

membrane which bounded the ovisac on its inner surface. That the yellow coat is still vascular at this time is proved by the fact mentioned in the preceding page.

In proportion as the entire generative organs subside into a quiescent state, so the remaining changes in the ovary take place more rapidly. The yellow colour of the ovisac passes into a paler hue, and at last into white. The radiating cicatrix may still be traced for some time longer, until, at the end of four or five months after delivery, every appearance of this structure has ceased to be discernible.

Certain physiological questions intimately connected with the foregoing history of the development and involution of the ovarian follicle may now be briefly considered. And first it may be asked—

Does the discharge of ova from the ovary take place independently of sexual intercourse, or of any kind of influence from the male?

This question has long ceased to be agitated with reference to animals lower in the scale than the Mammalia. It need, therefore, now only be considered in its relation to the latter, including Man. And since many have recently undertaken to prove that Man and the Mammalia constitute no exception to the general rule that in all classes of the animal kingdom which produce and emit ova the act of emission of ova is independent of the male, so, whatever form the inquiry may now take, it would naturally have for its chief object the determination of the value of the evidence upon which such an assertion has been based.

Now, the facility with which the process of ovulation may be observed in animals justifies the expectation that in such a case the amount of objective proof, collected by those who have undertaken to establish a law of spontaneous ovulation in Mammalia, would be sufficient to prove that law beyond the possibility of question. But when we turn to the principal writers who have devoted their attention to this point, with the view of collecting and critically examining such evidence, it must be confessed that the result is productive of a certain feeling of disappointment at the form in which the facts have been recorded, and the circumstances under which the observations and experiments have generally been made.

This is more particularly felt when, after examination of the evidence adduced, an unhesitating acceptance of the law, as one of universal application, is demanded. Before, however, the question of universality is considered, it will suffice, for the purpose of proving the possibility of a spontaneous ovipont, to give one or two examples in which all the conditions necessary to establish this fact were observed, viz., absence of coitus, rupture of the ovarian follicle, and the presence of the unimpregnated ovum in the oviduct.

The following case is related by Bischoff.* A lamb which had never received the male, and which had exhibited signs of "heat" about an hour previously, was shut up alone. On the following morning the male was admitted (for the purpose of testing the heat). He several times showed a desire for the coitus, but was prevented. The animal was killed the same afternoon, when it was found that a Graafian vesicle in the right ovary had burst. The spot did not project from the surface of the ovary, but attracted attention by the circle of red vessels surrounding the small opening which constitutes a familiar appearance in dogs and rabbits after bursting of a follicle. The diameter of this opening was about $\frac{2}{5}'''$. As a matter of precaution, search was made for spermatozoa, in order to obtain the negative certainty that no coition had taken place, but none were found. The infundibulum contained a thread of mucus intermixed with granules resembling those of the membrana granulosa. The Fallopian tube was next carefully examined, and at a distance of $5'''$ from its entrance was found an ovum still surrounded by the cells of the granular disc, and possessing all the characters of the unimpregnated ovarian ovum.

But since in this instance the presence of the male was permitted, though coitus was prevented, as was also the case in one half of the instances recorded by Bischoff in his celebrated Treatise from which this example is quoted, it may be well to notice another observation taken from Raciborski †, in which this possible objection was removed.

A bitch which had never been covered, and was just commencing to be in heat, was kept shut up for eight days, apart from other dogs. It was then killed. Only one ovary was examined, the other having been laid aside and forgotten. Three large follicles of a lively red occupied the entire surface of the ovary. One of these follicles was already shrunk, and presented at its summit a distinct fissure. In each cornu of the uterus, an ovum, the size of a poppy-seed, was found, surrounded by bloody mucus, — the one at a distance of about $2\frac{1}{4}$ inches, and the other at $\frac{3}{4}$ of an inch from the extremities of the tubes. Doubtless, if the other ovary had been examined, at least one follicle would have been found to have opened there also.

In order to show that the same process of discharge of the ovum, independent of sexual congress, may take place in the human subject, a case, recorded by Dr. Letheby, may be here quoted*:—"The body of a lunatic, aged 23, who had died in St. Luke's Hospital, was examined. She had been a patient in that institution for eleven months, under circumstances which deprived her of the opportunity of associating with a male for a long period before her death. It was ascertained that the girl had quitted life during a menstrual period; the cavity of the uterus, and the Fallopian tubes, contained a red, jelly-like secretion. On the outer and lower part of the right ovary was a dark livid spot, in the centre of which was a hole. On making a section of the ovary so as to divide it through the spot and an adjacent cicatrix, it was perceived that the hole led into a cavity which was surrounded by a dark-red tissue, and that the cicatrix communicated with a very perfectly-formed *corpus luteum*, having a central cavity containing a dark-red clot. In the right Fallopian tube was discovered a little globular body of the size of a pin's head. This was seen, under the microscope, to consist, in its outer surface, of a mass of nucleated cells. At one end of this mass was a transparent ring, enclosing a rather opaque granular mass, in which there was an eccentric spot." The author had no doubt that this was the ovule consisting of the zona pellucida, yolk, and germinal vesicle. In another case related at the same time, and where the hymen was perfect, similar results were obtained.

The possibility of a spontaneous ovipont having been established by these and like instances which might be quoted, it becomes important next to determine how far the law just enunciated is universal in its application; we may therefore inquire, —

Does the discharge of ova from the ovary always take place spontaneously, and independent of sexual intercourse?

It is in endeavouring to determine this question, so far as the attempt has been made to base this law upon observations and experiments on animals, that the difficulty to which I have just adverted is experienced; for, whilst there is no lack of argument upon the subject, it must be confessed that the number of well-recorded instances proving a spon-

* Beweis, p. 24. See next page.
† De la Puberté, p. 376.

* Phil. Trans, 1852, pt. i. p. 5.

taneous ovipont in mammals is exceedingly small.

It will suffice for illustration to observe the manner in which this question has been handled in the celebrated works of Bischoff*, Raciborski†, Coste‡, and Pouchet.§ The first only of these authors has given in detail the observations and experiments upon which he has endeavoured to found a law of spontaneous ovulation in the Mammalia. In several of these the coitus was permitted; and although it is rendered highly probable, from the circumstances narrated, that in some this had no effect in producing the discharge of ova, yet the introduction in any form of the only condition that could vitiate the experiments detracts certainly from their value. In five, however, of Bischoff's experiments it was known that coitus had not occurred, and in three of these ova were found discharged, accompanied by the usual appearances in the ovaries indicative of the recent rupture of the follicle.|| In a fourth case, the state of the ovaries left no doubt that the ova, which could not be found, had escaped; while a fifth case was examined before the ova had escaped. To these Bischoff adds an example of the ovipont in an animal, in which it was only probable that no coitus had occurred.

The work of Raciborski contains a single example, which has also just been quoted.

The works of Coste and Pouchet contain no examples of a spontaneous ovipont in animals, but the observations of each of these authors are given in the form of results. Each work contains a minute description of the process of ovulation, drawn apparently from separate observations; but these descriptions are not accompanied by any detailed examples, nor any statement of the means used to render these observations proofs of an ovipont, independent of coitus.

But all these authors agree in stating that ovulation occurs independently of sexual union, whilst they differ as to the degree of strictness with which the universality of this law is enforced. Pouchet demands that the law should be received without any exception, and observes with surprise the "unaccountable vacillations" of those among his predecessors who yield to it only a partial assent.

But in the absence of any extensive series of well-recorded observations, whose numerical force shall be such as to compel a universal acceptance of the law, it is not surprising that some who regard it as having been too hastily framed, and as too rigid in its exclusiveness, should withhold their full assent to it. For let it be conceded that the ova, when they have attained their complete development, escape naturally from the ovary, the rupture of the follicle not necessarily requiring the intervention of the male, should it therefore be inferred that the latter is completely inoperative when exercised on opportune occasions?

In this form the question is put by Coste, who maintains that although the coitus may not be the essential cause of the rupture of the follicle, yet it undoubtedly has the power to precipitate that event, and even to prevent its failure. He further considers that there is this difference between the fecundated female and one in whom impregnation does not take place; that in the former the rupture of the follicle is prompt, whilst in the latter it is tardy, or even in certain cases fails to occur.

In order to support this view, Coste cites two observations upon the rabbit. In the first of these, the animal was in heat, and manifested great ardour for the male, but coitus was not permitted. It was kept for forty-eight hours, and then killed. The genital organs were highly congested. Six follicles in one ovary, and two in the other, were apparently ready to burst, but no rupture had yet taken place. In the second experiment, the animal remained in heat for three days; on the fourth day the heat ceased, and on the fifth it was killed. The organs were in the same condition as in the last case, but no follicles had burst. Coste attributes the absence of rupture in these cases to the prevention of the coitus at a time when, if permitted, it would in his view have determined that event.

In whatever light these observations may be viewed, they are important as showing that an animal may sometimes advance far in the period of heat, and even pass through it without any ova escaping from the ovary; but it would require a very much greater number of parallel observations to prove by such negative results the effects of the sexual congress in determining the act of the ovipont. And it is matter for regret that this point has not been more clearly determined; for whilst no satisfactory results can be looked for from any observations upon this part of the subject in Man, this is eminently a question capable of being determined by experiments on animals. All the earlier observers who directed their attention to the condition of the ovaries in relation to reproduction bear unconscious testimony to the fact that the time at which the ova quit the ovaries bears no strict relation to the act of coition. Barry states that, taking the coitus as the starting-point of his reckoning, he was obliged to sacrifice a score of rabbits before he succeeded in meeting with one instance of the ovum at a particular time after its escape, and he had almost given up the attempt in despair.

If means be used to prevent the contact of the seminal fluid with the ova after their discharge from the ovary, or to prevent its arrival at the latter organ before rupture of the follicle, this does not affect the immediate condition of the follicle. The number of ruptured Graafian vesicles which have been found, after experiments made by placing ligatures upon

* Beweis der von der Begattung unabhängigen periodischen Reifung und Loslösung der Eier, &c. 1844.

† De la Puberté, et de la Ponte périodique. 1844.

‡ Histoire du Développement. 1847.

§ Théorie positive de l'Ovulation spontanée. 1847.

|| One of these cases is given above.

the tubes before coitus was permitted, has usually amounted to the sum of the ova discharged. If one side of the uterus be tied, the ova found in that cornu will not have been impregnated, but those on the free side will be developed. The number of ruptured follicles in each ovary will agree with the number of ova found in the corresponding tubes; but no difference will be perceptible between those on the impregnated and those on the unimpregnated side of the uterus. The contact, therefore, of the seminal fluid with the ovary has nothing to do with the discharge of the ova, or with the formation of a " corpus luteum." The only question that can here have place is, whether the excitement of the coitus, or the contact of the seminal fluid with the inner surface of the vagina and uterus, has any influence in precipitating the discharge of ova from the ovary when they are ripe for impregnation. This, however, is, in the present state of our knowledge, an unsettled point. By all the earlier observers down to Barry, it was assumed that the coitus was the sole determining cause of the ovipont. By most physiologists since that time the coitus has been regarded as having nothing to do with the discharge of the ova, or only a limited power has been ceded to it, as in the view of Coste just detailed.

So far as numerical amount of recorded observation goes, it may be asserted that the spontaneity of the act of emission of ova, independent of sexual intercourse, has been more fully and satisfactorily proved in Man even than in animals. In the works and essays upon this subject, to which reference is given in the preceding page, a large amount of evidence will be found; but since some proofs of this fact have been already given, and since it is proposed again to return to the subject in considering the question of menstruation in its relation to ovulation, it will not be necessary to pursue the subject further here. (See page 666.)

In tracing the process of ovulation, it will have been observed that the ovarian follicle passes through a series of changes, so gradually progressive and of such a definite character, that the knowledge of these may be turned to great account in any investigations relating to the ovipont; for, next to the discovery of the ovum itself, whether in the ovary, Fallopian tube, or uterus, the condition of the capsule, from which it is about to be or has been already discharged, will afford the best evidence as to its probable locality and condition, even should the ovum not be found. Doubtless, one of the greatest impediments which has been encountered in investigations of this class arises from the extreme difficulty, and often the impossibility, of finding the ovum in many situations on account of its minute size. Hence, in the absence of this demonstrative evidence, which cannot always be obtained, any other, which, though only inferential, may be made available for a like purpose, is of great value. Wanting the ovum, therefore, the state of the ovicapsule may be made, in part at least, to supply the evidence which is deficient. Now it has been shown that, whatever affects the ovum, to determine its development or the converse affects in a like degree the follicle from which it had been discharged, not on account of any apparent sympathy between the ovum and the follicle which once contained it, but from the whole generative track being more or less brought under the power of one common stimulus, felt alike by all the parts that are employed for the nutrition and protection of the ovum. It will be desirable, therefore, now to determine what evidence the condition of the ovarian follicle affords, first, as to the previous escape of an ovum, and secondly as to the probability or certainty of that ovum having been impregnated or otherwise. But since it is desirable to fix the value of certain terms which are commonly employed to designate particular states of the follicle, it will be needful, first, to determine,

What is a corpus luteum?

This term, as Raciborski has observed, is indicative of the infancy of science. It belongs to a period when anatomists were in the habit of designating by the word body or *corpus* any part of the animal economy whose nature or relation with other parts they did not comprehend, adding to this some distinctive title drawn from the general appearance of the part. Hence the terms *corpus striatum*, *corpus callosum*, *corpus luteum*. It is an unfortunate circumstance that such a term was ever applied to the Graafian follicle, and the more so since it is often employed without any definite meaning.

The Graafian follicle in its progress towards full development, and previous to its rupture, has been described as becoming yellow. This fact has been long known. It is stated by Home, Baer, Valentin, Wagner, and Bischoff. The cause of the yellow colour has been fully explained. After impregnation this yellow colour becomes still more conspicuous on account of the greater thickness of the ovisac or inner coat of the follicle, which is the seat of the change producing this colour. From the greater distinctness, larger size, longer duration, and other peculiarities of the follicle after impregnation, an artificial distinction has been made between the follicle in this state, and all other forms of it, in which it exhibits the yellow colour. The former are arbitrarily called "true," and the latter "false" *corpora lutea*. But there is as little reason for the use of the last term, as there would be for denominating a child a false man; for that which is commonly designated the "true" *corpus luteum* is the follicle in its largest condition of growth, as it appears after impregnation; whilst in all other conditions, when it has not been stimulated to full growth by impregnation, and whether before or after rupture, it has been called a "false" *corpus luteum* so long as it possesses the yellow colour. This distinction, therefore, as far as regards the terms employed, is not only unscientific and arbitrary, but is calculated to mislead by suggesting the idea that the so-called "true" *corpus luteum* is a totally different body from the "false," whereas these terms actually represent the same body, only in different stages of growth or decay. But practically it becomes a question how far it may be possible to determine, from the physical appearance of the follicle, whether impregnation has taken place. And this question is a very important one, especially in its obstetric and forensic bearings.

From the account already given of the several stages of growth and decay of the ovisac, it will have been seen that the yellow colour is common to all these alike, with the exception only of the earliest and the very latest stages. It alone, therefore, can afford no distinctive evidence upon the subject. But, in combination with other signs, the yellow colour, by its extent, may be made available to distinguish those cases in which impregnation has occurred; for when this is the case the ovisac, as stated, continues to increase in thickness; a greater abundance of yellow deposit takes place in its tissues; the follicle, instead of shrinking and disappearing in the course of one or two months, continues to be visible for fourteen or fifteen months. It acquires a new coat which lines its cavity, or else this cavity is entirely closed by a coagulum which becomes organised and solid; it presents the convoluted appearance which gives it a resemblance to the cerebral convolutions, and this convoluted condition gradually passes into one which is characterised by the presence of rays proceeding from a centre. Finally, the whole body constitutes a resisting and more or less solid mass, which can at once be detected by the touch, before the ovary is opened. The distinctions, therefore, are chiefly those of degree: the greater solidity; the greater thickness of the yellow walls; their more marked convolutions; the long persistent cavity, round or oval at first, and subsequently stellate; the milk-white membrane lining the cavity, when the latter exists, or the white dense mass occupying its place, resulting from the transformation of the clot. These last characteristics of the so-called true corpus luteum, viz., the cavity lined by the white membrane or the solid white centre, as well as the large central stellate cicatrix, may be regarded as absolute and not comparative distinctions, for they are not found in the follicle in process of involution when impregnation has not taken place.

With regard to scrofulous tubercles, which have been often enumerated among "false corpora lutea," it is probable that some of the conditions of the ovisac now described have been hastily set down to this score, without sufficient examination; for although scrofula may possibly affect the ovary, as it does the testis, yet a formation there of distinct scrofulous tubercles, unless they are abundant in other parts of the body, is, I am satisfied, a rare, if not an unknown, occurrence. No doubt, however, need at any time exist as to the nature of such bodies, since, if the bright yellow colour of the ovisac is not sufficiently marked, as in those cases where they have become pale, and more nearly approaching the buff colour of tuberculous matter in general, the microscope will at all times determine the question, for in respect of composition there is nothing in common between tuberculous matter and the ovisac in any of its natural stages of growth or decay.

Setting aside morbid states, nothing is ever seen in the perfectly healthy ovary except the stroma and ovisacs or Graafian vesicles in different stages of development or decline. These may be arranged in three series:

Ascending Series.

1. The simple undeveloped ovisac, before it has acquired an indusium from the stroma of the ovary, or from the walls of an already developed follicle, in which it may be formed. It requires at this time the microscope for its examination (*fig.* 373.).

2. The ovisac after it has acquired its outer capsule, by union with which it has become a Graafian follicle.

3. The Graafian follicle of the size of a hemp seed, or rather larger. It contains oil granules in the coats of the ovisac, but not yet in quantity sufficient to produce a yellow colour. In this state numerous follicles are seen in sections of every healthy ovary during middle life (*figs.* 370. and 372.).

4. The follicle when it is approaching the surface of the ovary. It is enlarging, and its inner coat or ovisac has now a yellow colour.

5. The ripe follicle which is about to rupture and discharge an ovum. It is always found at the surface of the ovary, projecting often to a distance of 3-4‴. It is covered by numerous veins, and in the centre of the most prominent part the coats of the follicle, as well as the ovarian coverings, are thinned and partly absorbed. Their thinness permits the contents of the follicle to be partly visible, and thus is produced a brownish red colour at this spot. The follicle contains blood or a bloody fluid, and sometimes a clot. The cavity is of considerable size, 4-6‴. The inner coat is of a bright yellow colour, and exhibits slightly wavy folds (*figs.* 380. and 381.).

6. The follicle which has already ruptured. An irregular lacerated opening extending ½-2‴ is perceptible in the centre of the attenuated part, through which the ovum, together with that portion of the membrana granulosa which lay beneath the seat of the rupture, has escaped, or is about to escape. The follicle is beginning to collapse. Its walls, no longer distended, become folded into numerous small plaits, producing, on section, the appearance resembling cerebral convolutions. The cavity is consequently diminished. It is empty, or contains a little bloody fluid or a clot (*fig.* 385.).

Descending Series. A. Not pregnant.

7. In the follicle which has recently burst, shrinking has commenced. The yellow ovisac is much plicated. The cavity contains a clot which is becoming pale, and exhibits under the

microscope distinct fibrillation, or the cavity is empty and much contracted.

8. The shrinking having rapidly progressed, the ovisac exhibits deep plications, and the rays are beginning to form, but the yellow colour is still distinct.

9. The cavity is nearly or entirely obliterated. The yellow colour is gone, but the rays remain, and the collapsed follicle now forms a white stellate body with a small central point (*fig.* 372. *h*).

10. The follicle itself is reduced to a mere point in which none of the foregoing characters can be traced.

Descending Series. B. After Impregnation.

11. The follicle has not materially diminished in size. The lacerated opening is closed. The yellow coat is much plicated, and the clot when present shows fibrillation, as in No. 7., or the cavity is empty.

12. The follicle has acquired greater firmness and solidity. The yellow ovisac is much increased in thickness. The folds are not so numerous, but are deeper, though not quite so distinct. Vessels contained between the folds appear to pervade the yellow coat. The white lining of the cavity is formed, and within it is a clear fluid, rather viscid, (*fig.* 387.), or the centre of the yellow ovisac is solid, and exhibits no cavity.

13. The central cavity is nearly or entirely obliterated. In the latter case a solid white body occupies its place, extending into the yellow mass in divergent rays. This arises from the plication of the white lining, by which process the cavity is closed. The colour of the principal mass is now a dirty yellow; it is somewhat reduced in size, and its outline is oval or irregular (*fig.* 389.).

14. The more prominent features observable in the last condition may still be faintly traced. In size the body measures 2-3‴. It is of a pale white, and is chiefly distinguishable from the surrounding stroma by the absence of vascularity in its tissues. Its solidity is gone.

To return, then, to the two questions which led to the foregoing considerations as necessary to their solution, viz.—

What evidence does the condition of the ovarian follicle afford, first, as to the previous escape of an ovum, and secondly, as to the probability or certainty that that ovum has been impregnated or otherwise?

It may be concluded that whenever the follicle presents the appearances exhibited in the first series down to and including No. 5., the ovum has not escaped; although it may not be detected, either on account of the difficulty of finding so small a body, or else because it may have perished by absorption or decomposition.

In the condition No. 6., an ovum has just escaped, or is in the act of escaping. None of these conditions of the follicle afford the slightest evidence of previous impregnation. They have all been repeatedly observed both in Man and animals where the coitus has never occurred.

Between No. 7. and No. 11. it may be difficult to draw a positive distinction. No conclusion regarding the question of previous fecundation, derived from the state of the follicle during the first fortnight after the escape of an ovum, would be absolutely safe; although the difference between the unimpregnated and the impregnated is such as to afford in every instance at least strong presumptive evidence, for the follicle shrinks rapidly in the former, while in the latter it undergoes little or no diminution in size.

But after this period there can be no question as to the prior occurrence of a fecundating coitus. Every follicle presenting the conditions described in Nos. 12, 13, and 14 has discharged an ovum, which has been afterwards impregnated. Every follicle in the states described in 8, 9, and 10 has discharged or has contained an ovum which has perished. But this proves only that fecundation has not occurred. It affords no evidence whatever that the coitus has not obtained.

Lastly, it may be observed that if, as is sometimes the case, the follicle fails to complete the process of rupture after the first steps of preparation have been made, the ovum may perish or be absorbed without being discharged, and the follicle will then shrink and become obliterated, as in the first series of changes. And it is further noticeable that although the number of Graafian follicles exhibiting the appearances indicative of the discharge or fecundation of ova, may generally be taken to represent the number of ova also actually discharged or fecundated, yet this will not always furnish a safe guide, because one follicle may contain two ova, or one or more ova may have escaped the influence of the coitus which had fecundated the rest. The number of ruptured or altered follicles therefore will in the first case be less, and in the second greater, than the number of ova or fœtuses found in the oviducts or uterus.

Development and Involution of the Ovary.

The Origin of the Ovary, and the Alterations which it undergoes at different Periods of Life.

The ovary takes its origin in a separate portion of blastema, quite independently of the Wolffian body, with which it is in close contact. It is not indeed until after the development of the Wolffian bodies has made considerable progress, and about the time at which the kidneys first appear, that, according to the observations of Bischoff on the mammalian embryos generally, the ovaries are first perceptible.

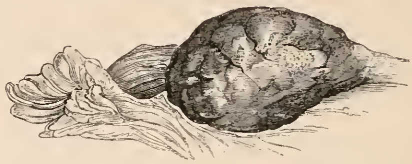
In the human embryo the ovary cannot be discerned earlier than the 5-7th week. Nor is it possible at the time of its first appearance to distinguish the ovary from the testis. Hence the term "generative gland" has been proposed by Kobelt as the most appropriate designation for a structure which, according to him, is then capable of being converted into either organ indifferently. In a human embryo of the fourth week, of which I have given a description in the Transactions of the

Microscopical Society of London *, no trace of an ovary or generative gland was discoverable, but only slight indications of two linear-shaped bodies occupying the dorsal and lumbar regions on either side of the vertebral column, representing the corpora Wolffiana. In another embryo measuring 5‴ in length, the generative gland could just be discerned in front of the supra-renal capsules and kidneys, but its form could be only indistinctly traced. In an embryo, however, which measured 8‴ in length, the gland had already assumed distinctly the elongated figure characteristic of the early formation of the ovary. It measured 0·8‴, and its position was oblique, or intermediate between the perpendicular direction of the Wolffian body and the horizontal one of the fully formed ovary. In an embryo of three months the generative gland or ovary still retained the oblique direction. Its length was 2‴, and its breadth 0·4‴.

From this period the gland, which now begins to assume more decidedly the character of an ovary, gradually acquires the horizontal position in which it is found at birth (*fig.* 440.). In the fœtus at term the ovary has usually attained a length of 4-5‴, and a breadth of 1½-2‴ (*fig.* 441.). Its figure is an extended oval, with flattened sides and base. These meet to form a triangle, whose basal margins are sinuous and sometimes indented. At the age of three years, (*fig.* 442.) the ovary attains a length of 10-12‴, still however preserving its elongated form, with irregular or slightly indented margins. This peculiarity of a fœtal condition the ovary gradually loses as the period of puberty approaches, when it grows more rapidly and acquires the form and dimensions already described as characteristic of the mature organ (*fig.* 369.). At this period of life, however, no feature of the ovary is more subject to variation than its form. Even for some time after the catamenia have been established, the elongated figure is often seen to have been retained, although the rounded or gibbous outline is more commonly observed by the time that adult age is attained.

The ovary is now full and plump ; its surface up to the time of puberty has remained uniformly smooth, even, and shining, and its investing tunics are unbroken.† But it has been seen that, from puberty onwards, through these two tunics of the ovary, the ova periodically escape by a process of dehiscence, resulting from an absorption and rupture of these tunics. The effect of these repeated lacerations is twofold. The surface becomes scarred in all directions by the closing up of

Fig. 390.



Ovary about the time of cessation of menstruation. (*Ad Nat.*)

the lacerated openings, whilst the successive discharges of the contents of the ovisacs gradually diminish the bulk of the entire organ (*fig.* 390.). In proportion as age advances, these cicatrices and indentations become still more numerous, and the once smooth and plump ovary is converted into a small corrugated wrinkled body full of pits and tortuous

Fig. 391.

Ovary in old age. (*Ad Nat.*)

lines (*fig.* 391.). When sections are made of the ovary in this condition, it is found that all traces of the Graafian follicle have disappeared; or one or two only may be observed, degenerated into little masses or sacs of cartilaginous hardness. More commonly, however, nothing now remains but a dense parenchyma.

Besides these changes in the form of the ovary and the condition of its component parts, great alterations also take place in its vascular supply. In early life, and especially from the establishment of puberty up to the critical age, the organ is abundantly supplied with blood-vessels, which are seen everywhere both in the proper parenchyma of the ovary, and also upon the walls of the ovisacs. These have been described as undergoing enlargement, and probably increasing in number in the neighbourhood of the spot at which the rupture of the follicle occurs. Not only, however, is there a local hyperæmia in these situations at each recurrence of the ovipont, but the entire ovary receives a larger supply of blood on these occasions. But when the process of ovulation has entirely ceased, the tissues begin to suffer the wasting of age, the ovary partakes in the general state of pallor of the other pelvic viscera, and the ovarian vessels carry only as much blood as will suffice for the bare nutrition of the shrivelled organ.

* Vol. iii. part ii. p. 65.

† In reference to the human subject, the universally received opinion regarding the discharge of ova by rupture of the ovisac, as an occurrence which commences only at or after puberty, has been called in question by Dr. Ritchie, who, after detailing a series of observations upon the condition of the ovary at various periods of life, asserts that "the Graafian vesicles contained in the ovaries prior to menstruation are found, as they also are in every other period of life, in continued progression towards the circumference of the gland, which they penetrate, discharging themselves by circular-shaped capillary-sized pores or openings in the peritoneal coat; the presence of the catamenia being thus no indispensable prerequisite to their rupture."[1] It should be observed, however, that the facts adduced by Dr. Ritchie do not appear to bear out very clearly the conclusions which he has drawn from them.

[1] Lond. Med. Gaz., vol. xxxiv. p. 253.

ABNORMAL ANATOMY OF THE OVARY.

Effects of extirpating the Ovary.— A natural deficiency of the ovary together with the oviduct of one side is known to prevail in the class *Aves*, but this deficiency, which is occasioned only by a want of development of one half of the generative organs previously existing entire in the embryo, does not affect the reproductive power of birds.

Mr. Hunter, wishing to determine the effect of extirpating one ovarium upon the number of young produced in Mammalia, procured two young sows of the same farrow, and having removed a single ovarium from one of them, he kept both animals under the same circumstances, in order to observe the comparative effects of breeding upon them.

They commenced breeding when two years old. The spayed animal took the boar earlier than the perfect female, and both continued to breed at nearly the same times.

The spayed animal continued to breed until she was six years old, and in that time she had eight farrows, producing in all seventy-six pigs, but she did not take the boar afterwards. The perfect sow continued breeding until she was eight years old, and had thirteen farrows, yielding one hundred and sixty-two pigs. She then ceased to breed. The result therefore of this experiment was, that the perfect animal continued to breed two years longer, and produced in all ten more than double the number of the spayed one, although she had not double the number of farrows.

But few opportunities have occurred for observing the effects produced by the removal of the healthy ovaria upon the human female.

The case in which Mr. Pott removed both these organs at the same time constitutes the best example on record.

A young and healthy woman, twenty-three years of age, was received into St. Bartholomew's Hospital, on account of two small swellings, one in each groin, which had for several months been so painful as to prevent her from following her occupation as a servant. The swellings, which were not inflammatory, were soft, uneven upon their surface, and moveable. They lay directly upon the outside of the tendinous opening of the oblique muscle through which they appeared to have passed. The woman was in full health, was large breasted, and menstruated regularly. On account of the inconvenience occasioned by the presence of these tumours in the groins, Mr. Pott was prevailed upon to remove them. They were found upon examination to be the two ovaria which had descended in the form of a double inguinal hernia. The woman subsequently enjoyed good health, but became thinner and more apparently muscular; her breasts, which were large, were gone, nor did she ever menstruate after the operation; the last observation of her having been made several years subsequent to that event.*

Deficiency of the Ovary. — Complete congenital absence of both ovaries, except in the case of the non-viable fœtus, is of extremely rare occurrence. It is almost always associated with deficiency or imperfect formation of the uterus, and generally with incomplete development of the vagina, nymphæ, clitoris, and mammæ. The sexual appetite in these cases is wanting. Menstruation is absent; the secondary sexual characters are but feebly expressed, and there is of necessity a total inaptitude for reproduction.

The ovary may, however, be deficient on one side only, without any of these accompanying conditions. There may be nothing externally to mark the defect, nor is there necessarily here any impediment to the exercise of the sexual function.

Arrest of Development. — The ovary, like the uterus, long retains its infantile condition, but as the period of puberty approaches it expands and soon attains its full size. This change, however, may not occur. The ovary may cease to grow after the third or fourth year, and, under these circumstances, the whole organism manifests a corresponding tardiness of development. An interesting example of this is preserved in the museum of King's College. The preparation consists of the entire internal organs of a young woman who died at the age of nineteen without having menstruated. The ovaries, as well as the rest of the organs, are no larger than those of a child of three years (see *fig.* 465.). In these cases the mammæ are small, the external organs only partially developed, and the whole frame is formed upon a feeble scale.

Atrophy and Hypertrophy. — Atrophy has been shown to be one of the conditions at which the ovary inevitably arrives when a certain period of life is passed. It is under these circumstances a normal condition, just as the state last described is also a normal condition when associated with a certain epoch, but both become abnormal states when they occur out of their usual course. Thus, an early atrophy of the ovary on both sides will of necessity bring with it a premature failure of procreative power, although an atrophied state of the organ on one side only, like atrophy of one testis, will but little, if at all, affect this power.

Of hypertrophy of the ovary a more particular account will be given in the description of morbid growths and abnormal developments of its special parts.

Displacements of the Ovary. — The ovary, in consequence of its peculiar mode of attachment to surrounding parts, enjoys great freedom and range of motion. This is rendered most conspicuous, when, during the gradual enlargement of the gravid uterus, the ovary is carried upwards from the pelvic into the abdominal cavity. Under these circumstances the ovary certainly vindicates the character assigned to it by the older anatomists, of being an appendage to the uterus, for it necessarily follows the movements of the larger organ to which it is attached. Thus, the ovary is sometimes a pelvic and sometimes an abdo-

* The Chirurgical works of Percival Pott, by Earl, vol. ii. p. 210.

minal viscus. But it may be displaced from its normal position in either of these cavities under various circumstances. The causes of such displacements are chiefly, inflammation of the surface of the ovary terminating in adhesions, displacements of the uterus, and herniæ.

As a result of inflammation of its peritoneal covering, the ovary may be bound down to the side of the uterus, or Fallopian tube, to the recto vaginal pouch, to the brim of the pelvis, to the colon, to the convolutions of the ileum, or to the omentum.

The displacements of the uterus which occasion a dislodgement of the ovary from its normal position are, retroversion, inversion, and procidentia, or complete prolapsus.

In retroversion the ovaries are carried downwards along with the uterus into the hollow of the sacrum, where they occupy a position on either side of the principal organ. In inversion of the uterus, the ovaries, together with the Fallopian tubes, fill the interior of the artificial pouch, which is formed by the reversement of the organ ; whilst in extreme prolapsus the ovaries, together with the uterus, escape almost entirely from the pelvis, and occupy the sac which is formed by the inverted vagina.

But the most remarkable displacements are those in which the ovary constitutes a true hernia. Such a hernia may consist of the ovary only, or may include other organs, as the Fallopian tubes, uterus, intestine or omentum. A true hernia of the ovary alone is of comparatively rare occurrence. It may happen on one or on both sides, and may be either congenital or acquired. The celebrated case of Mr. Pott was an example of a double inguinal ovarian hernia. And this appears to be the form under which this singular displacement has been most frequently met with. In these cases the ovary constitutes a solid tumour of the size of a pigeon's egg, which may be detained at the ring, or lie within the inguinal canal, or even descend to the labium.

An example of this kind of hernia, in which the left ovary has for many years occupied the inguinal canal, has recently come under my notice. Deneux *, who was at the pains to search out all the cases on record up to his time, has collected examples also of crural, ischiatic, umbilical, ventral, and vaginal hernia of the ovary, and to these Kiwisch has added a case of hernia through the foramen ovale.

Diseases of the Tunics.

Inflammation of the ovarian tunics, and particularly of the peritoneal coat, is most commonly associated with acute puerperal metritis. But inflammation, both in the acute and chronic form, may affect the ovary independently of the puerperal state. The resulting anatomical changes in the coats of the organ are vascular congestion in various degrees ; fibrinous exudations upon their surface, followed occasionally by the formation of artificial bands or adhesions with surrounding parts ; and chronic thickening of these coats, whereby the original smooth and even surface, (*figs* 368. & 369.) characteristic of the ovary in early life, is lost. When inflammation of the ovary has advanced to the suppurative stage, and this organ is converted into a bag of pus, the coats may have become so attenuated and softened as to burst when the attempt is made to lift the parts from the body after death.

Ulceration. — *Rupture.* — In the case of large collections of fluid within the ovary, as for example in large abscesses or in ordinary ovarian dropsy, the surface of the ovary frequently inflames and contracts extensive adhesions with surrounding parts, and if the latter happen to be hollow viscera, such as the intestines, uterus, or bladder, a fistulous communication may be established between them and the sac of the ovary, through a process of ulceration or absorption of the common partition wall, and the contents of the ovary may become discharged externally. Or it may happen that by a similar attenuation and rupture, or by a process of ulceration and absorption of these tissues, the ovarian walls give way, in some parts of their free surface, and their contents escape into the abdominal cavity.

Hypertrophy of the ovarian tunics is almost constantly observed in considerable enlargements of the organ, from whatever cause they may arise. In the case of large ovarian cysts, before adhesions have been occasioned by the pressure of surrounding parts, the peritoneal coat of the ovary, though much thickened, retains its smooth, shining, external surface. It may be generally stripped off with ease, and displayed as a dense white membrane of unequal thickness, but having undergone no further change than that of a general hypertrophy of its ordinary component tissues. The tunica albuginea in like manner becomes thickened by simple increase of its ordinary constituents, but in the case of very large, and particularly of unilocular cysts, the cyst wall becomes so intimately blended with the common ovarian investment, that it is impossible to determine how much of the now united membranes was originally furnished by the tunica albuginea, or ovarian stroma, and how much by the proper wall of the cyst. The hypertrophy in these cases is often so considerable that the boundary walls of a large ovarian cyst may measure one or two inches or even more in thickness in some places.

Ossification. — Patches of ossific matter more or less extensive are occasionally found scattered over the surface of ovarian cysts. It is probable, however, that these are deposited in the first instance upon the inner surface, or in the proper walls of enlarged cysts, and subsequently extend to the proper coverings of the ovary, and that the fibro-cartilaginous degeneration which these cyst walls sometimes exhibit, also commence in the original cyst, and proceed from within outwards.

Diseases of the Tissues.

Hyperæmia of the ovary may be limited to

* L. C. Deneux, Recherches sur la Hernie de l'Ovaire. 1813.

the parenchyma, or to the walls of particular follicles, or may affect all these parts together.

Hyperæmia of particular follicles, with considerable enlargement of the sac and effusion of blood into the cavity of the follicle, is not unfrequently observed as an abnormal condition. But hyperæmia of single follicles with effusion of blood into the cavity has been already described, as being also a natural state of the Graafian follicle, which is preparing for dehiscence and discharge of an ovum.*

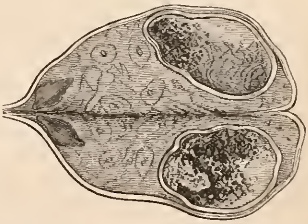
It may be asked, therefore, in what respect does the normal differ from the abnormal state, and by what characteristics may the one be distinguished from the other? It appears to me that Rokitansky, in the account which he has given of hyperæmia of the Graafian follicle †, has included under one head both the natural and the morbid condition; for his description will very well apply to the rising follicle, in its second stage, when the escape of blood into the cavity has been shown to be a normal, and in some animals a constant occurrence. The presence, therefore, of blood within the follicle, for the reasons already fully given (p. 556.), must not be regarded as necessarily affording evidence of a morbid state. There are, however, certain peculiarities in the condition of the unhealthy follicle, by which it may be distinguished from that which is natural. The natural follicle, when preparing for dehiscence, is always near the surface, and often projects considerably above the level of the ovary (*fig.* 380.). Its coats are unequally thick; the thinnest portion being always found at the most prominent point of the follicle. There is considerable vascularity about this point, plainly visible externally, and here the process of attenuation and absorption continues to be progressive until the sac spontaneously ruptures. The walls of the follicle are at this stage of a *bright yellow colour.* The liquor folliculi is either clear and limpid or intermixed with blood, or the centre of the sac is filled by a coagulum, which is at first bright red, and afterwards becomes pale, and at length nearly white. The coagulum may adhere to the walls, and undergo fibrillation and subsequent conversion into a solid body, or into a dense white membrane, or it may be rapidly absorbed.

On the other hand, the morbid follicle, although it may not exceed nor even equal in size that which is passing through its normal changes, may yet be distinguished by many characters which are the converse of those just described. The morbid follicle is often not peripheral, but is more or less central in its position in the ovary. It may attain to the size of $\frac{1}{3}$ or $\frac{1}{2}$ of the ovary, without necessarily causing any distinct prominence above the surface (especially when occurring singly). The walls are equally thick, and exhibit at no part any evidence of attenuation or absorption. No preparation for rupture is indicated externally by any peculiar arrangement of vessel, or by any marked increase of vascularity. The walls do not exhibit the remarkable yellow colour nor the cerebral foldings characteristic of the advancing normal ovisac, but the tissues of which they are composed are simply those of the undeveloped Graafian follicle. The contents of the sac are neither the clear liquori folliculi, nor the bright clot, nor the decolorised fibrin, but generally a collection of dark coffee-ground matter, resulting from the admixture of a quantity of decomposing blood-corpuscles and fragments of membrana granulosa intermixed with a dirty fluid. On washing out these contents, the walls of the cyst, if the ovary has been injected, are seen to carry numerous vessels, irregularly arranged, but never presenting that rich network of capillaries which are visible after a successful injection of a healthy ovisac progressing towards rupture, especially in those cases where the quantity of yellow oil is not so great as to obscure these vessels altogether.

By these characteristics the morbid ovisacs may generally be distinguished from those which are healthy. There is enough of similarity between them to prove their identity of origin, and enough of dissimilarity to show their divergence from a common starting point; the healthy follicle proceeding onward through a course of different changes, which have been already fully described; the morbid follicle exhibiting an apparently unlimited power of growth and deformity, such as will be presently more fully noticed.

Fig. 392. exhibits the morbid follicle in one of its earliest stages of growth. It may be contrasted with *figs.* 381. and 385., for the purpose of showing the points of difference which have just been described. In *fig.* 392. the morbid follicle occurs as a single cyst in the midst of

Fig. 392.



Ovary containing a morbidly distended Graafian follicle in an incipient stage. The rest of the organ is healthy. (*Ad Nat.*)

otherwise healthy tissues. Although occupying more than $\frac{1}{3}$ of the entire ovary, it scarcely disturbs the even outline of that organ. Its coats are of uniform thickness throughout. There is no attenuation nor preparation for dehiscence at any particular spot, nor external sign of increased vascularity in one point. But the walls of the follicle contain numerous vessels, distributed nearly equally over their surface. The cavity is filled with loose flocculi of a dark chocolate colour, consisting of decomposing blood clot mixed with patches

* P. 556.

† Manual of Pathological Anatomy. Sydenham Society. Vol. ii. p. 328.

of membrana granulosa. The walls of the follicle are not yellow, and contain no oil globules. They are slightly thicker than those of the healthy follicle. Their component tissues are precisely those which have been already described as characterising the ovisac in its normal condition; the chief bulk of their texture being made up of granules and embryonic fibres intermixed with a few developed fibres of ordinary white fibrous tissue.

Such a condition may, for want of a better designation, be regarded as hyperæmia of the follicle, or it might perhaps be more appropriately termed hypertrophy of the follicle; but in whatever light it may be regarded, it constitutes one of the early stages of those enormous growths, of which more will be said hereafter.

A more extensive form of congestion, affecting the parenchyma of both ovaries, and associated with a like hyperæmic condition of the uterus, may be sometimes observed about the period of the final cessation of menstruation. The ovaries are then occasionally found of an intense red colour, from the parenchyma, as well as the follicular walls, being deeply loaded with blood. The most marked instances of this I have observed in connection with cardiac disease, and associated with congestion of other organs.

Inflammation of the Ovary.— Ovaritis.— Oophoritis.—Our knowledge of the pathological changes which the ovary undergoes as the result of inflammation, is chiefly derived from examination of the bodies of women who have died of acute puerperal metro-peritonitis. But unquestionably inflammation both in the acute and chronic form may affect the substance of the ovary, independently of the puerperal or pregnant states, and cause various degenerations of the tissues of that organ, as evidenced by those serous, fibrinous, and puriform deposits, or general softening of the ovarian parenchyma, which are occasionally found after death. It is probable also, from symptoms displayed during life, that inflammation, especially in a chronic form, not unfrequently attacks the ovary and terminates in resolution, or in those milder results of inflammation which consist in temporary induration or enlargement of the organ, unaccompanied by serious disintegration of its tissues.

It must, however, be observed with regard to the evidences of inflammation of the ovary either in the acute or chronic form, which are supposed to be afforded during life, consisting in pain and tenderness referred to the seat of that organ, or in obvious enlargements of the ovary, as discoverable by various modes of internal or external tactile examination, and conjoined with more or less constitutional disturbance, that these signs may and do often in the non-puerperal state, accompany the natural process of ovulation, and that such symptoms, recurring with each menstrual period, may affect a woman at intervals in a greater or less degree during the whole of that period of life in which she is capable of childbearing. But in the present state of our knowledge of ovarian processes it is perhaps not possible to determine how much of these symptoms may be regarded as evidence of a natural, and how much of a morbid change in the part; for although in many women the process of ovulation is continually performed without consciousness of local suffering, yet in a great number of instances the act is accompanied by much pain, and there can be no question that the cause of much of this suffering is to be looked for in the changes which the tissues of the ovary undergo in the act of expelling the ova.

How closely this process in its more obvious conditions is allied to inflammation has been already shown. A high degree of vascularity of the part, with increased exudation of fluid, and consequent enlargement and tension of the entire organ terminating in spontaneous laceration of its coats by a process very similar to ulceration, and often accompanied or preceded by a more or less considerable escape of blood: these together form a combination or series of processes closely allied in their nature to inflammation, and frequently evidenced externally by signs usually regarded as characteristic of inflammatory action.

Nor is it yet known how far these symptoms, which have generally been assumed to indicate ovarian inflammation, especially in a chronic form, may be merely the external evidences, not of natural, but of aberrant or disappointed ovulation. For just as an abscess is painful generally in exact proportion to the unyielding nature or tension of the parts by which it is surrounded, so it is probable that when the follicle or the entire ovary becomes tense from the effusions which have been shown to have taken place ordinarily within it, and this tension is not relieved because rupture does not occur at the proper time, so that ovulation is disappointed or is aberrant, the symptoms which might be expected to accompany such an interrupted process would be those which are usually set down as indicating inflammation in a part.

This matter appears hitherto to have been hardly thought of, and yet it is probable that to *abortive or interrupted ovulation* may be referred the commencement of many of those morbid conditions of the ovary which are not either malignant or the direct results of inflammatory action. Probably many of the cystic diseases of the ovary originate in this way. Of disappointed ovulation, as it may be observed in animals, instances have been given at page 568. Here the follicles, although apparently preparing for rupture, were arrested in their progress from some unexplained cause; and although it may be conjectured that such follicles might, under an increase of stimulus, accomplish their final purpose, as Coste has supposed in reference to the instance just quoted, yet it has been shown by the researches of Barry that multitudes of ovisacs perish without accomplish-ing that purpose at all, and it is probable that these, in preference to other and more healthy follicles, become the seat of subsequent morbid changes.

For it must be remembered that the circumstances under which the male and female generative elements escape from the place of their original formation are essentially different. The male secreting organ, the testis, is provided with an excretory duct for the escape of the fertilising fluid ; but the female gland is a shut sac. To the normal escape of its products many barriers are opposed, and it has already been shown by what complicated machinery the shedding of the female product is effected. But it is impossible to regard this complex process without perceiving how easily a failure in any of those steps may defeat the final object for which that process is set on foot. The thickness of the walls of the follicle, the density of the ovarian coverings, or of the parenchyma of the ovary, if the follicle should fail to reach the surface ; the chance of the ovum perishing before it quits the ovisac, and so the stimulus to the healthy development of the latter being lost ; the chance of an excessive accumulation of liquor folliculi or of blood within the follicle, causing damage to the ovum, and replacing a natural by a morbid amount of exudation. In these and other possible interruptions to the natural completion of ovulation we may discover the elements of many future morbid changes. And although it would require a long continued and deep research into the aberrant functions of the ovary to determine the true order and sequence of many of these morbid processes, yet it is impossible to carry anatomical investigation into the structure of the morbid ovary, especially under incipient forms of disease, to any extent without many fragmental observations occurring suggestive of the idea that the ovary, like any other gland, may have its natural functions impeded, and that many of the organic changes which are observed in this part may owe their origin to such interrupted processes. Some of the observations which have led me to the adoption of these views have been already given, and some others will be detailed as suggestive of a better basis for the study of ovarian pathology than has hitherto been employed ; for of all the organs of the body the ovary is perhaps that whose pathological conditions have been regarded with the smallest amount of reference to its natural or deranged *functions*.

From these considerations, then, I have been led to the conclusion that certain conditions of the ovary, which, from their concomitant symptoms during life have been deemed inflammatory, are not necessarily associated with inflammation ; that it is probable, first, that the natural process of ovulation is often accompanied by symptoms very similar to those of inflammation ; and secondly, that the process of ovulation is occasionally disappointed or interrupted, and that the follicles, whose natural development has been interrupted, may, like the hydatiform placenta, become the seat of a low form of nutrition, terminating in effusion and collection of various dropsical fluids.

With regard to the anatomical evidences of inflammation of the ovary as furnished by post-mortem examination, they are chiefly the following, viz.: general redness or hyperæmia of the ovarian parenchyma, or of the walls of the follicles ; swelling of the ovary to the extent of increasing the organ to three or four times its natural size, producing a round, oval, or flattened form of the ovary ; a general tension or hardness of the organ in the early stages of inflammation, and subsequently softening, consequent on degeneration of the tissues and their infiltration by serous or puriform effusions; and lastly, but rarely, gangrene of the ovary.

Of these morbid changes the only one which appears to require a more particular account is

Suppuration of the ovary. Pus may be found in a circumscribed cavity within an enlarged and highly vascular ovary, portions of whose structure may still retain its natural condition. Or the entire ovary may be converted into a bag of pus, the natural tissues being entirely destroyed, and the fluid bounded only by the ovarian tunics. In such cases the abscess "appears to rise from suppuration in the substance of the viscus, similar in every respect to phlegmonous abscess in any part of the body, and not connected with any cyst, or change, or addition of structure, the product of morbid growth."* These abscesses, which are sometimes of enormous size, may burst into the general sac of the peritoneum, or, after forming adhesions with surrounding parts, may discharge their contents externally through the abdominal walls, or into the Fallopian tube, uterus, vagina, bladder, rectum, or other part of the intestine. Portal mentions cases of ovarian abscess as large as an infant's head, and Dr. Taylor † of Philadelphia has recorded an instance in which the ovary contained twenty pints of pus. It is highly probable that these and even still larger collections of pus, which have been found in the ovary, were, as Mme Boivin has suggested, originally cases of encysted ovarian dropsy, but inflammation and suppuration having been set up in the walls of the cyst, the original contents have been gradually intermixed with pus, until the whole fluid has appeared to be of that nature. Probably of this kind also was the case recorded by Vater‡, in which the ovary was as large as the human head, and "contained pus distributed into several capsules." This, therefore, was a multilocular abscess.

Except in connection with acute metro-peritonitis, suppuration of the ovary may be considered as comparatively rare. Dr.

* Seymour's Illustrations of some of the principal Diseases of the Ovaria, p. 40.

† North Amer. Med. & Surg. Journ. 1826.

‡ Haller, Disp. Med.

Hooper* "met with only two instances of abscess" of this organ. "The one was the size of a child's head at birth, the other not larger than an orange. There was nothing in these different from common abscesses; the whole of the internal substance of the ovaries was gone, and the walls were formed of a thick and rather ligamentous cyst, covered by peritoneum." Suppuration occurs also occasionally in those cysts of the ovary which contain hair and teeth, together with other imperfectly formed products. To the same class of suppurative diseases should also probably be referred that singular morbid condition of the part in which the entire ovary is reduced to the state of a diffluent pulp, of a yellow or brownish-green colour, of the consistence, and having somewhat the appearance of very soft putty, immiscible with water, and retaining sufficient tenacity to preserve its semifluid character, and yet not having firmness enough to admit of the part being preserved as a preparation. Of this morbid condition of the ovary, which, however, may possibly be cancerous, I met with a striking example in a case of sudden death occurring in the seventh month of pregnancy. Both ovaries were of the size and form of a bullock's kidney, their natural structure was entirely destroyed, and was replaced by the soft substance just described. The circumstance that both ovaries were thus affected renders it evident that the disease could not have existed in any great degree at the time of impregnation, or that it certainly must have been then limited to one organ.

From the comparatively scanty materials extant relating to ovarian abscess it may be concluded, that suppuration may either commence at separate parts of the parenchyma, forming small collections of matter, which gradually coalesce, or it may be set up throughout the whole of the stroma at once. In these cases the parenchyma of the ovary is gradually consumed, and the organ is converted into a purulent cyst.† Whilst in other cases the Graafian follicle appears to be the seat of the suppurative action, which may either commence originally in the walls of one or more follicles constituting circumscribed abscesses of moderate size, or the suppurative stage of inflammation may be established in the walls of a follicle already considerably enlarged, and thus an ordinary ovarian cyst, with simple transparent contents, may be gradually converted into an abscess of enormous magnitude.

Cysts.—A complete anatomical description of the numerous forms of cystic disease which affect the ovary would occupy a far larger space than the limits of this article will permit. On this account the more important varieties only can be noticed. These are chiefly Simple cysts, Compound cysts, Hydatid cysts, Demoid cysts, or those containing fat, hair, teeth, and bones, and Colloid cysts.

Simple Cysts.—The simple, barren, or unilocular ovarian cysts are composed, as their name implies, of a single sac, which, according to its size, occupies the interior of the ovary, whilst the rest of the organ retains its normal condition; or else the cyst, by enlarging, presses aside and distends the parenchyma and tunics of the ovary, which thus form a common boundary to the sac, or the cyst, having originated in one extremity of the ovary, grows at the expense of that portion of the organ, whilst the rest, retaining its natural structure, becomes by degrees a mere appendage of the sac, and may be seen projecting in the form of a small button-like prominence from its outer surface.

These cysts vary in size from that of a pea to the bulk of the adult head; they rarely, however, attain the latter dimensions without becoming proliferous or multilocular, and they appear never to acquire as single cysts the enormous bulk which the compound cysts not unfrequently exhibit. This more moderate size of the single cyst is less frequently productive of those adhesions with surrounding parts which the pressure of the larger compound cysts so commonly occasions. Hence the precise locality of the single cyst, and its origin in the substance of the ovary, can generally be determined without difficulty. The distended sac is found hanging as an appendage to the ovarian ligament, whilst the Fallopian tube is often seen partly spread out over its surface, one of the fimbriæ being always closely adherent to the sac, and conducting the observer infallibly to any portion of the original ovarian structure which may have remained yet unchanged.

The coats of these cysts vary much in density and thickness. Those of the single kind are more uniform throughout; they are generally thickest towards the base or seat of their vascular supply. Here they vary in thickness from 2‴ to 12‴, but become much thinner in other parts, so as at times to be nearly transparent. The outer coat always consists of peritoneum, which is smooth and shining upon its surface, except when adhesions have been formed with surrounding parts, or when fatal peritonitis has occurred, as from bursting of the sac. The condition of this coat has been already described under the head of morbid states of the ovarian tunics. The variations in its thickness are not generally so considerable as materially to affect the bulk of the sac.

The middle or intermediate coat is that generally upon which the greater or less density of the cyst wall depends. This coat is usually of a brownish-yellow colour, and firm fleshy texture. It is with difficulty split into a number of rough-surfaced laminæ, exhibiting to the naked eye a coarse fibrous arrangement of their constituent parts, which, under the microscope, are seen to consist of inelastic fibrous tissue, mingled with granules, and undeveloped fibre cells in varying proportions.

* The Morbid Anatomy of the Human Uterus and its Appendages, p. 3.

† Rokitansky, Path. Anat. vol. ii. p. 331. Syd. Soc. edit.

To this coat, which appears to retain or increase its thickness by a perpetual new formation of fibrous tissue, is due that support and resistance to the pressure of the increasing contents of the sac, which prevents the more frequent rupture of these cysts. And it is probable that when the latter phenomenon occurs, without the formation of previous adhesions, followed by ulceration, the laceration is due to the gradual attenuation of the middle wall of the sac.

Occasionally portions of these walls are found to be of nearly cartilaginous hardness, so that they can with difficulty be broken up into fragments for minute examination. Such portions are seen under the microscope to be composed almost entirely of close-lying fibres of white fibrous tissue, with scarcely a trace of the embryonic fibres and granules, which are found abundantly in the walls of the softer cysts, and of the normal ovisac. Other portions of these cyst walls, still more dense, present to the naked eye, as well as under the microscope, all the characters of the simpler forms of cartilage; whilst in the walls of other cysts again are found patches of ossific matter, in which the earthy elements of bone are aggregated together, (calcification) but without the definite arrangement characteristic of true osseous structures.

Upon and in the substance of this middle coat ramify numerous arteries and veins, sometimes of considerable magnitude. These distribute their minute branches upon the inner surface of the cyst, where they occasionally present a peculiar straight or rectangular arrangement. Doubtless these vessels are the carriers of those enormous collections of fluids which accumulate within the cysts, and upon their arrangement, as well as upon the nature of the epithelial lining of the sac, depends probably the character of the fluids secreted or effused.

Most variable is the condition of the lining membrane which bounds the inner surface of the cyst. In the smaller cysts it is often composed of one or more layers of simple flattened epithelial cells; the remains, perhaps, of the membrana granulosa. This surface may be free, or to it may adhere fragments of blood clot, degenerating or undergoing fibrillation, by which the sac, when small, is partly filled. This lining of epithelial cells is often seen in a state of fatty degeneration*, and similar cells are found abundantly scattered among the contents of the sac.

In the larger and older cysts the membrane lining the sac is nearly as smooth as that which covers it externally. In these the lining membrane often exhibits but little vascularity, and shows small traces of an epithelial covering in its smoother parts, where it is usually so intimately adherent to the middle walls, as to be separable from the latter only with difficulty. Fragments so obtained are easily split up, and are seen to be composed of developed fibres of connective tissue, intermixed with fine granules and a few embryonic fibres.

After the simple cyst has arrived at a certain period of its growth, and generally when it equals the size of a large orange, it begins to exhibit upon its inner surface patches, more or less extensive, of rough projections, granulations, or vesicles, which will be described more fully under another section.

Multiple Cysts.—I have employed this term to designate a variety of the single cyst which might be confounded with the compound or proliferous kind, and which consists merely in an aggregation of two or more simple cysts that have been contemporaneous in their growth. The distinction between a mere aggregation of simple cysts and the growth of a compound one has been carefully drawn by Rokitansky*, and has been also illustrated by Paget.†

If such cysts are observed at an early period of their growth, they may be seen to occupy different portions of the ovary in which they arise independently of each other, and having distinct portions of ovarian stroma interposed between each. They have at first a round or oval form, but "as they all enlarge together, and sometimes by the wasting of their partition walls come into communication, they are flattened by reciprocal pressure, and "may at length look like a single many-chambered cyst, having its one proper wall formed by the extended fibrous covering of the ovary. Many multilocular cysts, as they are named, are only groups of close-packed single cysts; though when examined in late periods of their growth, and especially when one of the group of cysts enlarges much more than the rest, it may be difficult to distinguish them from some of the proliferous cysts.

Figs. 392. and 393. serve to illustrate the simple and the multiple cyst respectively. *Fig.* 392. has been described at p. 575, where this example is given as an instance of hypertrophy of a Graafian follicle in an early stage, forming a simple or unilocular cyst, still hardly contained within the substance of the ovary. It will be seen that at one part of this preparation the wall of the cyst has become blended with the general investments of the ovary; and it will be easily understood how, by the gradual enlargement of the cyst in this direction, where there will be the least amount of resistance to its growth, the sac may at length become so greatly expanded that the remaining healthy portion of the ovary will appear only as an appendage to it, or may become by pressure and extension altogether obliterated. *Fig.* 393., taken from Dr. Hooper's collection ‡, offers a good example of the multiple cyst. It is composed of a mere aggregation of simple or unilocular cysts, which, by coincident enlargement, have come at length to fill the entire ovary, causing considerable increase in bulk of that organ. From the right ovary (*a*) a portion has been removed

* Wedl, Patholog. Histol. p. 461. Syd. Soc.

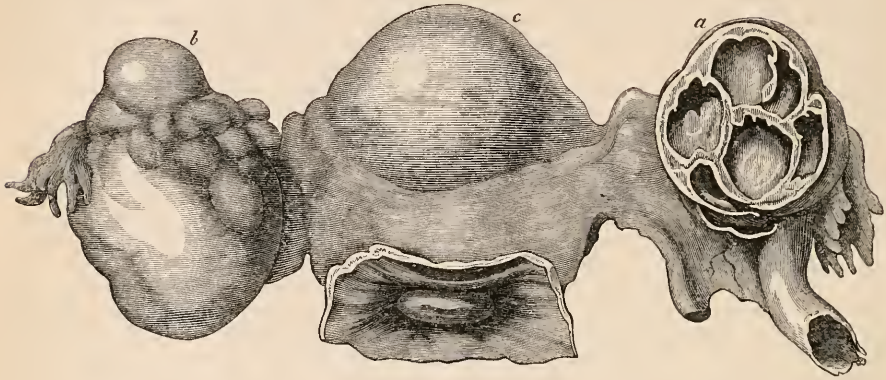
* Loc. cit. p. 332.

† Lectures on Surgical Pathol. Vol. ii. p. 56.

‡ Morbid Anatomy of the Human Uterus.

exhibiting a section of several simple cysts of nearly equal size; whilst the left ovary (*b*) shows a similar alteration of texture, the organ being still unopened, and exhibiting numerous small sacculi which have here begun to project above the surface.

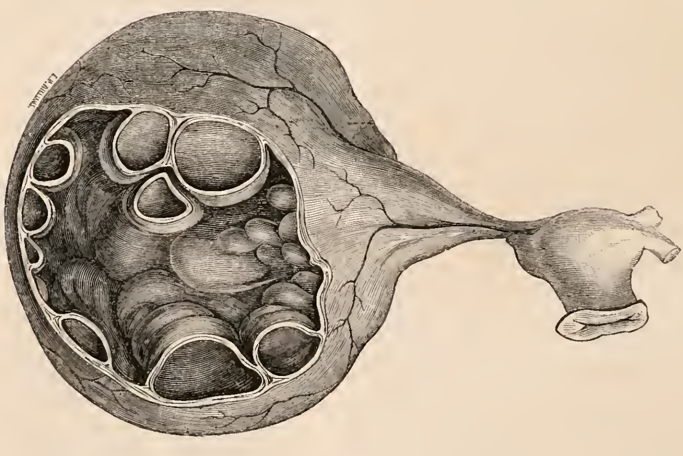
Fig. 393.



a, right ovary, exhibiting numerous unilocular cysts, consisting of enlarged Graafian vesicles; *b* left ovary similarly affected, but unopened; *c*, uterus. (*After Hooper.*)

Multilocular, Compound, or Proliferous Cysts.—In these a second, or, it may be, a third, order of smaller cysts are developed, within or upon the walls of a larger or parent sac. From these walls the secondary cysts, at a comparatively early period of their growth, are seen projecting inwardly in hemispherical form, arranged along the parietes of the sac, from which they commonly spring by broad bases. These secondary cysts are invariably and permanently attached to and continuous with the walls of the superior cyst. They are covered by a continuation of the same membrane which lines the principal sac, and which is reflected over them in the same manner that the heart is invested by the reflected pericardium, or the testis by the tunica vaginalis.*

Fig. 394.



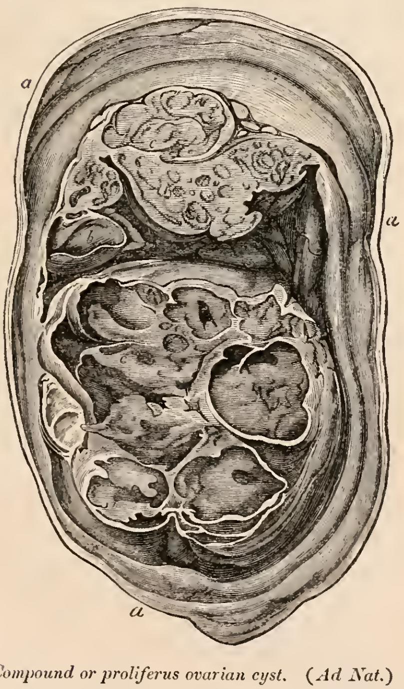
The left ovary distended into one large cyst, into the interior of which project numerous smaller cysts of a secondary order. To the right of the figure is the uterus. (*Ad Nat.*)

* Hodgkin, Lectures on Serous and Mucous Membranes. Lect. viii.

The growth of these secondary cysts with broad bases, of which a good example is exhibited in *fig.* 394., is often very irregular, so that one or more of them enlarging with greater rapidity than the rest, encroach upon the cavity of the containing cyst, and fill it more or less completely. This rapid enlargement of the secondary cysts also occasionally causes rupture of their walls and the escape of their contained fluids into the parent cyst, followed by the unrepressed growth of the secondary or tertiary cysts which arise from its surface.

After the appearance of a tertiary order of cyst within the secondary ones, their growth occasions so much disturbance of the even outlines of the walls in which they originate, that it is often difficult to trace the order and manner of enlargement of the different series. Nevertheless, with care, these may be often made out even in the complex forms, of which *fig.* 395. furnishes an example. Here is represented a small portion only of an enormously enlarged ovary, consisting of a primary or principal sac, the greater part of which has been cut away, so as to leave a part of its walls visible at *a*, *a*, *a*, and of a more solid basis which was made up of numerous secondary

Fig. 395.



Compound or proliferus ovarian cyst. (*Ad Nat.*)

a, *a*, *a*, divided walls of the principal single cyst; *b*, small simple cyst; *c*, *c*, two masses of compound secondary cysts, containing many of a tertiary order.

and tertiary cysts. Both of these orders may be traced in this example. At *a*, *a*, *a* are seen the divided walls of the original parent cyst, whilst springing from these walls at *b* is a single secondary cyst, and at *c*, *c* are two groups of similar cysts aggregated in masses. The latter are, however, examples of compound secondary cysts, for in the interior of each is contained a series of a tertiary order, which are so numerous as to fill completely the secondary sacculi. By Lebert it is deemed to be still an open question whether these cysts, which apparently spring from the interior of the main sac, as represented in *figs.* 394. and 395., are altogether new formations, or whether they were not originally in part developed, and by force of pressure, arising from contiguity of situation, have penetrated and at length grown within the principal cyst, into the interior of which, in this view, therefore, they would form a species of hernia.

Dr. Hodgkin *, whose elaborate descriptions of ovarian cysts has made known all the principal varieties of form which they assume, distinguishes from the broad-based cysts, already noticed, those which arise by narrow or slender peduncles. These sometimes grow from the walls of the principal cyst, and, indeed, in almost all cases which I have examined, after the sac has attained a certain size, patches of these pedunculated sacculi may be observed scattered over the interior in various places, but they are more constantly observed growing from the interior of the secondary cyst. These little sacculi appear at first in scattered patches, under the form of little round grains, thickly covering the lining membrane which they raise above them, and so closely set that two or three hundred may sometimes be counted in the space of a square inch. When these elongate, mutual pressure causes them to assume a filamentous condition; but when greater freedom of growth is enjoyed, their extremities commonly dilate into little pouches, or buds of another order sprout from the sides and extremities of the original growths, and convert them into a multitude of little dendritic processes which roughen the inner surface of the larger cysts, or fill more or less completely the cavities of the smaller ones.

If a section be made of these dendritic processes, they are seen usually to be solid at their base, the white fibrous tissue of the parent cyst wall, from which they spring, being easily traced into their stems and branches. But at their extremities they become dilated into little pouches filled with fluid, similar to the little pediculated cysts, with which they are abundantly intermixed. These little cysts and processes are covered by epithelium, and it is probable that they are the active agents in the elimination of the various fluids by which the ovarian cysts, of whatever order, are commonly filled. These minute processes and vesicles, so abundantly found on the walls of endogenous cysts, are represented in *fig.* 396., which exhibits a portion of a proliferous cyst of the natural size, covered by them on its inner surface.

* Loc. citat. and Med. Chir. Trans. Vol. xv. pt. ii.

Fig. 396.

Part of the thick laminated wall of an ovarian cyst, covered on its inner surface with pyriform vesicles. (After Paget.)

The Contents of Ovarian Cysts.—No cystic formations in any part of the body present such a variety of contents as those which are found in the ovary. These vary in every degree of consistence, from the thinnest fluids to the hardest substances, such as teeth and bones. They may be subdivided according to their densities and different degrees of organisation. And first may be considered :—

The Fluid Contents of Cysts.—The thinnest fluids are usually obtained from unilocular cysts, which have not been previously tapped. The fluid so procured is commonly of a pale straw colour, and resembles in general character the ordinary fluid of ascites. It is to these cases that the term "encysted ovarian dropsy" is most commonly applied. The contents of multilocular cysts are often less fluent, presenting every variety of consistence from a thin gelatinous fluid to one of the density of white of egg, of honey, of thin size, or of soft glue. In the latter cases the tenacity of the fluid is often so great that it may be drawn out into long strings, and it is only in this way that it can be extracted through the canula. All these varieties, which commonly retain more or less transparency, may be found enclosed in different cysts within one common investment.

In other cases the contents, while retaining their fluidity, are rendered turbid or are thickened by the admixture of pus or of blood in various degrees. Thus are produced the yellow and green hues as well as the red, reddish-brown, and dark coffee-ground colours which these fluids often present; the turbid yellow and green colours being generally caused by the presence of pus, the bright red by the admixture of recent blood, and the dark brown or coffee-ground hue sometimes by the addition of blood which has been effused long enough to have undergone putrefaction, although the brown colour is not always due to this cause. Scales of cholesterine are also found intermixed with those fluids, and in the smaller cysts especially, as already stated, recent blood or the blood clot undergoing fibrillation, or breaking down by putrefaction, may be frequently noticed.

The repeated withdrawal of the contents of ovarian cysts affords the opportunity of observing that the fluid contained in the same sac often undergoes a material change in its composition. Thus, that which is obtained by a first tapping is often of the thin straw-coloured variety, whilst that which results from subsequent operations has more frequently the turbid muddy or coffee-ground character last described. This can be explained in two ways : the first, by observing that in multilocular cases there is sometimes a natural communication between the walls of the containing and the contained cysts, or an artificial communication may be established by spontaneous rupture, or by the trocar penetrating through two cysts, and thus the smaller will act as tributaries to the larger sac, and pour their varied contents into it; or secondly, inflammation or ulceration may be set up in the walls of a cyst which has been punctured, or the introduction of air, or of blood flowing into the cyst from vessels wounded during the operation may so modify the contents as to account for those successive alterations in the fluid which are very commonly observed. In the case of cysts containing pus, rough patches, apparently of ulceration, have been observed upon their internal walls.

Quantity of Fluids and Rate of Effusion.—The structure and situation of the ovary permit this organ to suffer a degree of distension which is rarely or never equalled in other parts. Probably the only limit to the increase in size of the morbid ovary, after it has risen out of the pelvis into the abdomen, is occasioned by the pressure which the spine, diaphragm, and abdominal walls exercise upon the cyst ; for the parietes of an ovarian cyst appear in most cases to possess an unlimited capability of multiplying the fibrous element of which they are principally composed, whilst the power of rapidly replacing the fluid after their contents have been drawn off, proves both the unrestricted capability of secretion inherent in the cyst walls, and at the same time the influence which pressure exerts in keeping that secretion for a time within certain limits. Numerous examples might be quoted in illustration of the immense power of growth and secretion of fluid possessed by ovarian cysts. Imhoff* records a case in which the right ovary contained 42 lbs. of fluid. Duret † met with 50 pints of water in

* Acta Helvetica, vol. i., App. p. 1.
† Mém. de l'Acad. de Chir. t. ii. p. 457.

a single ovarian cyst. And in the London Medical and Physical Journal (Aug. 1815) the particulars of a case are given in which the right ovary weighed nearly 52 lbs. But these are moderate examples compared with some of still larger growth. Camper* relates a case in which about 80 lbs. of serum were contained in the left ovary; and Douglas also one in which the left ovary held 70 lbs., besides a considerable collection of fluid in the pleura and pericardium.†

These enormous collections of fluid are generally limited to the ovary of one side, though both organs may be coincidently affected, as in the example given by W. E. L. Müller‡, who found in the body of a woman, aged 36, in the two ovaries together 140 lbs. of fluid. In what proportion either or both of the ovaries are affected by ovarian dropsy may be seen by reference to the tables of Safford Lee and Chereau. The former shows the right ovary affected 50 times, the left 35, and both together 8 times. The latter gives 109 examples of the right, 78 of the left, and 28 of both sides.

Notwithstanding the large amount of fluid which may collect within the distended ovary as shown in the foregoing examples, these yet serve to give but a feeble notion of the enormous quantities which may be effused from the walls of an ovarian cyst in the course of a lifetime, or even of a few years, when the contents are removed from time to time, and are allowed to re-accumulate. Pagenstecher§ removed, in 35 operations, 1132 lbs. of fluid, without reckoning what escaped by allowing the canula to remain. Dr. Mead's patient was tapped 67 times in five and a half years, and lost 1920 pints. Ford || punctured the ovary 49 times, and removed in all 2786 pints of fluid. Heidrich* in eight years punctured 299 times, and removed 3289 Berlin quarts (Berl. Maass), equal to 9867 med. pounds, the death of the woman occurring at the age of 43. And in the celebrated case of Mr. Martineau, of Norwich, in the course of twenty-five years the patient lost by tapping, in 80 operations, 6631 pints, equal to 13 hogsheads of fluid.

Composition of the Fluids contained in Ovarian Cysts.—Although these fluids usually coagulate freely in a greater or less degree on the addition of heat or nitric acid, the proportion of free albumen which they contain is usually considerably less than is found in the serum of blood; they contain, however, a larger quantity in combination with soda than is found in that fluid. According to the analysis of Dr. Owen Rees, who has examined several specimens of ovarian fluids, their chief characteristics are, a considerable excess of water and of extractives, and a deficiency of albumen as compared with the serum of blood. To the presence of a large quantity of extractives, particularly the albumen combined with soda, Dr. Rees attributes that peculiar tenacious mucoid character which these fluids so commonly possess. This is always in relation to the nature of the solid ingredients, and is quite independent of any peculiar proportions of water, to which at first it might be supposed to be due. Again, the alkaline salts obtained from ovarian fluids differ from those of blood in not containing any phosphate which can be recognised even as a trace, unless experiments be made upon large quantities for the express purpose of detecting that substance.

The following table †, by Dr. O. Rees, gives the results of the analysis of four fluids drawn from secondary cysts of an ovarian tumour, compared with an analysis of the serum of blood.

	No. 1. Clear, light straw-coloured Alkaline. Sp. G. 1017.	No. 2. Dark-coloured muddy neutral. Sp. G. 1017.	No. 3. Approaching in character to white of egg Alkaline.	No. 4. Clear straw-coloured, containing flakes of a pearly scaly-looking substance.	Analysis of the Serum of the Blood for comparison.
Water - - - - - -	190·9	190·70	195·2	187·7	181·2
Albumen with traces of fatty matter -	4·1	4·25	1·8	7·6	16·5
Albumen existing in solution as Albuminate of Soda - - -	3·7	3·62	1·1		0·4
Alkaline Chloride, and Sulphate, with Carbonate of Soda, from decomposed Albuminate - - - - -	0·8	0·78	1·2	4·0	1·6‡
Extractive, soluble in water and alcohol	0·4	0·45	0·5	0·5	0·3
Chloride of Sodium with Carbonate, from decomposed lactate of Alcoholic Extract - - - - - -	0·1	0·20	0·2	0·2	
	200	200	200	200	200

* Sammlung, bd. xvi. s. 562.

† Those who are curious in these cases will find instances referred to by Meissner (Die Frauenzimmerkrankheiten, Band ii.), in which a single ovary is said to have weighed 100, 120, and 150 lbs. respectively.

‡ B. v. Siebold's Sammlung, 1812, iii. Bd.

§ V. Siebold's Journ. für Geburtsh, b. vii. St. i. s. 93.

|| Medical Communications, vol. ii. 1790.

* Dissert. sistens Casum Memorabilem, Berol. 1825.

† From a valuable paper on Tumours of the Ovary, by Dr. Bright, in the Guy's Hospital Reports, vol. iii. p. 204.

‡ The whole of the Alkaline Salts are estimated together in the analysis of serum as indicated by the line.

So far, therefore, as these analyses may be taken to represent the ordinary composition of the more fluid contents of ovarian cysts, it may be concluded that the action performed in these cases by the walls of the cyst is the separation from the blood chiefly of the watery and saline ingredients, with the exception of alkaline phosphates, whilst the albumen is only in part removed, and none of the fibrine.

Examined by the microscope, the more fluid contents of ovarian cysts frequently exhibit flocculi, composed of patches of epithelium, more or less united together by granular matter. When gelatiniform they often contain faint oval corpuscles, or a few primitive corpuscles. Occasionally an opalescent or opaque creamy appearance is communicated to the jelly by the formation of pus corpuscles or minute granules, and sometimes the contents are wholly filamentous, and mixed with granular cells and other products of inflammation. This jelly-like matter, when consistent, presents all the characters of coagulated *liquor sanguinis*, which has not yet passed into organisation. Acetic acid develops in it, or causes to be precipitated a white membrane having all the characters of fibrous tissue. Frequently granules, cells, and filaments may be observed in it in various stages, as is the case with recent exudations from the serous membranes, or in other simple forms of hyaline blastema.*

Hydatids contained in Ovarian Cysts. — A very perfect example of this rare affection of the ovary (originally in the possession of Dr. Hooper) is contained in the Pathological Museum of King's College. It is the largest specimen of ovarian disease in that collection, and consists of an immense aggregation of compound thin-walled cysts, of the second and third order, many of the latter being stuffed full of hydatids. Several of these have fallen out of the cysts, and lie loosely at the bottom of the glass. They are of the form and average size of pigeons' eggs, and possess the usual characteristics of Acephalocysts. (Barren echinococcus vesicles?) Comparatively few cases of this form of ovarian disease are on record.

The solid Contents of Ovarian Cysts.—These consist of fatty matter, hair, teeth, and bones. Cysts containing such materials are termed dermoid cysts. They rarely grow with the rapidity, or attain the enormous bulk commonly observed in those with fluid or hydatid contents. That such cysts may, however, sometimes equal in size those of a more simple character, is shown by a remarkable example described by Blumenbach.† A girl aged 17 had a swelling of the left ovary, which after 21 years' growth measured four ells in circumference, and reached below the knees. Death occurred at the age of 38, when the sac of the ovary alone weighed 14 lbs., and contained also 40 lbs. of a thick, fatty, honey-like substance, mixed with short and long hairs, some two feet in length, and matted together in locks. Besides these the sac contained several irregular portions of bone, some of large size. In one of these were fixed six molars and one incisor tooth, completely formed. The inner surface of the sac was beset with short hairs.

The composition of these cysts, and especially of their lining membrane, will in a great measure account for the differences which are observable in their progress and mode of growth. The dropsical cysts are closely allied in their nature to serous membranes, and, like these in a morbid condition, they possess the power of separating and collecting into their cavities the thinner constituents of the blood. And as the only apparent limit to this process is the resistance offered by the walls of the sac, and the parts external to them, so the distensibility of these, and the capacity of the walls of the cyst to meet the increasing pressure by a correlative hypertrophy of its tissues, will determine the form, size, and general condition of the tumour. But the non-malignant cysts, whose contents are of a more solid nature, and possess a higher organisation, are tegumentary in their character. Their contents are chiefly tegumental products, which, once formed, have attained the limit of their growth. Such cysts, therefore, are more stationary in their character; or if occasionally they approach in bulk the watery cysts, as in the example just quoted, this arises mainly from the addition of a fluid secretion, and the necessity for circumscribing it by hypertrophy of the walls. But more often the cysts with solid contents, if they do not remain passive, contract adhesions with surrounding viscera, and by the aid of fistulous openings discharge their harder parts, such as bones, through the nearest natural orifice.

The tegumentary character of these cysts has been clearly shown by Cruveilhier*, Kohlrausch †, Lebert ‡, and Paget. § "Upon their inner surface is produced a growth of skin, with its layer of cutis, subcutaneous fat, epidermis, and all the minute appended organs of the proper hairy integument of the body;" whence the term "dermoid cysts." It is possible that at the commencement of their formation such cysts may have a general tegumentary lining, a part or the whole of which may afterwards become obliterated. For in the condition in which they generally come under our notice, the tegumentary structure is confined to patches of the lining membrane, while in many the hair is found entirely detached and lying in the form of a loose ball in the centre of a smooth-walled sac.

Sebaceous and Sudoriparous Glands have been shown by Kohlrausch and Heschl to be present in these cysts, where they have the same general arrangement as in the skin (*fig.* 397. *c*).

Fatty Matter. — This occurs under two forms: first, as a loose granular fatty sub-

* Dr. J. H. Bennett on Encysted Tumours of the Ovary and Pelvis, Edin. Med. and Surg. Journ. No. 167.

† Medicin. Biblioth. bd. i. s. 152.

* Anat. Pathol. tom. i. livr. xviii.

† Müller's Archiv. 1843, p. 365.

‡ Traité d'Anat. Pathol.

§ Lectures, vol. ii. p. 83.

stance, of the consistence and aspect of lard or butter, in the midst of which are imbedded those coils of loose hair with which it is usually associated (*fig.* 397. *d*). This fatty material is of a white or yellowish hue, and is commonly inodorous, but sometimes it exhales an intolerably fetid odour, especially in those cases where air has been admitted into the sac, and partial decomposition has taken place, or where fœtid pus has been formed within the cyst. The second condition under which fat is found is that of masses ½—1″ in thickness, lying beneath the general lining of the sac, which is protruded before them, causing irregular elevations into the interior of the cyst (*fig.* 397. *a*). These present the ordinary character of adipose tissue, but possess a smaller proportion than usual of the cellular element.

Hair is found in ovarian cysts also under two forms, either still attached to the walls or lying in loose tangled coils in the centre of the cavity. Those attached to the walls are seen to spring from follicles, which may be scattered evenly over the cyst wall, in which case the hairs are usually short, or they may arise from a group of hair follicles, closely set, and imbedded in a substance clearly possessing the characters of ordinary skin. In the latter case the portions of integument from which they spring are generally elevated upon a mass of subcutaneous fat, as just described, and the hairs, which are well nourished and long, form at their free ends a tangled coil, intermingled with the loose fat already mentioned (*fig.* 397.). In these cases the hair often attains to a considerable length; it is fine and smooth, and resembles the long hair of the back of the head, exceeding sometimes in length two feet. The colour of the hair is usually red, dark brown, or black; it bears no resemblance to the hair of the individual in whom it occurs. Thus, in the case of an ovarian cyst occurring in a negress, Andral observed numerous hairs differing essentially from the woolly hair of the head; they were soft, smooth, red, or blonde, and some were silvery, like the hair of children of white races.

The loose hairs may be easily detached by maceration in turpentine or ether, from the mass of fatty substance in which they are entangled. They are then sometimes seen to be destitute of bulbs. They are usually more crisp and shorter than the attached hairs, except when the latter occur singly.

Teeth are very commonly found associated with hair and fat. These may possess the perfect character of incisor canine or molar teeth, but more frequently the resemblance is only general, and a more accurate examination discovers in them some imperfection of form. The resemblance is sometimes greatest to the deciduous, and sometimes to the permanent set. In the less perfect forms the crowns only are developed, the roots being deficient. But in most cases the intimate texture of the tooth differs in no respect from the ordinary dental structure.*

Ovarian teeth are generally found associated with portions of irregular-shaped bone, in which they are often imbedded. They may, however, be attached to the tegumentary lining of the cyst walls, and more rarely they have been found connected to portions of cartilage.

Bone.—The bones found within ovarian cysts differ from the ossified portions occasionally observed in the cyst in this respect, that, while the latter consist of merely crystalline or amorphous aggregations of earthy matter, the former, although irregular in shape, yet exhibit a true osseous structure, in which may be readily detected the usual arrangement of concentric lamellæ, Haversian canals, lacunæ and canaliculi. Such bones often bear a sufficient resemblance to fragments of jaws and vertebræ to admit of a general comparison with those parts of the skeleton; but well-shaped and perfect bones are not found, except in cysts of whose nature and origin some doubts at least may be entertained.

In *fig.* 397. are represented several of the solid structures commonly found in an ovarian cyst. A long coil of tangled hair, mixed with lardaceous matter, is seen springing from a portion of the cyst wall at a part which is lined by common integument. Here many

Fig. 397

Ovarian cyst containing hair, loose fatty matter, adipose tissue, sebaceous glands, and hair follicles. (After Cruveilhier.)

hair follicles are observed, some being empty, and others containing short hairs. The parts

* This is illustrated by Plate 124. of Professor Owen's "Odontography," exhibiting the microscopic structure of a tooth, from an ovarian cyst in my collection. Five other teeth were contained in this cyst, together with a portion of tegumental structure, subcutaneous fat, bone, and hair.

of the cyst covered by integument are seen to be elevated, and it is in the substance of and beneath such elevations that the fatty tissue and bones are usually found imbedded, whilst the teeth have only their roots concealed, their crowns projecting free above the surface.

Origin of the Solid Contents of Ovarian Cysts.—It has been conjectured that these are examples of the "fœtus in fœtu," or that such remains may be the product of an imperfect ovarian conception. To the former of these suppositions, viz., that such formations result from a cohesion or intus-susception of two or more germs, coincidently impregnated, but of which one only has been perfectly developed, it may be objected that this view fails altogether to explain the circumstance that their formation occurs far more frequently in the ovary than in any other part of the body; nor does it account for the fact that here a particular class of structures only is developed, whilst in the case of penetration of germs one within the other, various portions of a second fœtus, more or less completely formed, and by no means limited to a certain class of structures, are found within the body of the first.

The explanation that these are examples of extra-uterine gestation of the ovarian kind is equally unsatisfactory; for even if the possibility of such a form of gestation be ceded, the fact alone that hair, teeth, and even bones, contained in cysts of the kind under consideration, are never found associated with the smallest trace of the membranes peculiar to the ovum, would be fatal to this view. But it can be shown further that such structures are observed in cases where previous impregnation was highly improbable, as in the examples where they were found in conjunction with a perfect hymen*, or where it was impossible, as in the case related by Dr. Baillie of a girl aged 12, whose generative organs were still undeveloped, but one of whose ovaries was filled with hair, teeth, and fatty matter.

The two additional circumstances that there is scarcely any portion of the body, such as the subcutaneous tissue, the brain, lung, kidney, bladder, and testis, in which similar structures have not been found, and that such formations, though most commonly found in the ovary, are yet not even limited to the female, but have been also observed in the male, completes the catalogue of objections to the argument, in whatever form it may be advanced, that these productions are in any way the offsprings of a spermatic force newly applied to the organisms in which they are formed.

The discovery of the fact that a tegumentary structure forms the basis out of which many of these products spring, appears to carry us a step further towards comprehending the mode in which some at least of the solid contents of ovarian cysts are formed, by exhibiting a connecting link between structures which are elsewhere naturally associated, but it obviously fails to satisfy any inquiry as to the nature or quality of the cell-force which determines the development of such products.

Fœtus, more or less perfect, contained in the Ovary(?)—Ovarian Gestation.—Graviditas Ovaria.—Few facts in physiology have been more readily assumed without sufficient examination than that the fœtus may be developed within the proper structures of the ovary, and so constitute a form of extra-uterine gestation.

So long as it was generally believed that the coitus was the efficient cause of the escape of the ovum from the ovary, and that therefore the act of impregnation preceded that of ovulation, there was nothing in such a belief to challenge inquiry as to the probability of the ovum being first impregnated, and still by some mischance detained within the proper structure of the ovary, where it might become developed. But more accurate views of the nature of ovulation and of the true seat of impregnation have led to a stricter inquiry regarding the seat of supposed ovarian gestation.

Among the earliest to call in question the accepted views upon this subject was M. Velpeau, who, previously a believer in ovarian gestation, laid before the Philomathic Society, in 1825, four examples supposed to be of this kind. An expression of doubts as to the possibility of this fact on the part of many members led to a more perfect dissection of the parts, in which examination MM. Blainville and Serres were appointed to assist. It was ascertained with certainty that three of the tumours were external to the ovary. With the fourth more difficulty was experienced; but at length, after isolating the Fallopian tube, which was sound, the detritus of conception was found to occupy a special sac between the peritoneal and proper coat of the ovary, which was entirely distinct.

In the following year, M. Geoffroy St. Hilares, in a report upon the subject of Breschet's Memoir upon "Interstitial" Extra-Uterine Gestation, expressed his entire disbelief in the ovarian variety, and the same views have been advocated by M. Pouchet in his work on Spontaneous Ovulation, and in this Cyclopædia by Dr. Allen Thomson*, who has there stated the general objections to the doctrine of an ovarian form of gestation.

The cases which appear to favour the belief in ovarian gestation may be divided into two classes, viz., those in which the embryo is yet small, and is contained in a sac of moderate size, which has not yet contracted adhesion with adjacent parts; and those in which the fœtus has attained or approached to full growth, and the sac by which it is surrounded has already contracted adhesions.

All the examples that I have had the opportunity of dissecting, or of seeing examined, have been of the latter class, and of these it may at once be said that nothing can be learned from them which could determine, with any degree of accuracy, so difficult a question as that under consideration.

* Royal Coll. of Surg. Pathol. Collect. prep. No. 2625.

* Vol. ii. p. 456.

The impediments to such determination which recur again and again in these cases are the following. It is easily ascertained that the sac containing the fœtus is external to the cavity of the uterus, and is in some way or other connected with some portion of the internal generative organs; the Fallopian tube, ovary, and broad ligament of one side being chiefly involved in the tumour, while the corresponding parts of the other side may remain free. Dissection may serve to unravel these parts to a certain distance, beyond which nothing satisfactory can be determined, on account of the alteration which the tissues have undergone both in form and arrangement; the hypertrophy of some, and the wasting or blending together of others, rendering further research fruitless for the object in view.

To these impediments, other and still greater difficulties are generally superadded. These arise from the death of the fœtus, which often takes place several months or even years previous to that of the mother. In the decomposition which follows, the harder parts of the contents of the sac fall asunder, and make their way by fistulous openings into surrounding viscera, whose surfaces inflame and give rise to serous and fibrinous effusion, while in the few hours which succeed to the final destruction, the parts decompose so rapidly that the post-mortem examination, however early it may be made, often reveals nothing but a semi-putrid mass perfectly unsuited to the determination of a difficult anatomical question.

For this purpose the cases of the former class can alone suffice. Here the parts are small, and as yet comparatively unchanged, and admitting of dissection. The results of four such examinations have just been given. The following additional examples, which are selected from the best recorded cases supposed to be ovarian, will suffice to exhibit the class of evidence upon which a belief in this species of gestation is demanded.

Cruveilhier* has described and figured a case in which the entire skeleton of a four months' fœtus † is seen hanging external to a sac, occupying the seat of the right ovary, in which it is supposed to have been once contained. The sac said to be in the inner and lower part of the ovary is lined by a serous membrane. The two external thirds of the pouch were filled by a spongy areolar yellowish-white mass presenting all the characters of placental tissue. The outer half of the surface of the ovary was enveloped in a cartilaginous shell. No attempt appears to have been made to trace the entire outline of the ovarian tunics, or to show the condition of the ovarian ligament, or of the Fallopian tube of the same side. The latter, indeed, is not mentioned, but from the representation of the parts it appears to be blended with the cyst, so that this is quite as likely to have been an example of tubal, or ovario-tubal, as of ovarian gestation. The fact also that the cyst had apparently burst and permitted the escape of the fœtus when it had attained the size which is seldom exceeded in tubal cases, lends additional probability to this view.

* Anat. Pathol. livr. xxxvi. pl. vi.

† Said in the description to be between one and a half and two months, at which time, however, no such complete skeleton is ever seen.

Dr. Granville * has published a case, accompanied by drawings, which he regards as an "undisputed case of purely ovarian fœtiferous ovum." The uterus is considerably enlarged, but empty. "The left ovarium presented a large swelling which contained within its own covering an ovum bearing a fœtus with all its appendages, of about four months' growth. The ovarian covering burst in three places, and allowed the protrusion of the ovum, whereby the adhesion of the placenta to the inner surface of the ovarian envelope was torn asunder," causing death by hæmorrhage. A blood-vessel, the size of a large crow-quill, which penetrated the dense portion of the tumour, was ascertained to be a branch of the left spermatic artery, and a smaller and much shorter vessel, arising from the tumour, was found to communicate with the spermatic veins. "The corresponding Fallopian tube was perfectly sound and loose, particularly at its fimbriated extremity, which had no connection whatever with the embryoferous tumour in its neighbourhood. Like its fellow tube, it was pervious only from its loose extremity inwards to about half its length. "A placental mass with distinct cotyledonous vesicles connects the child with the inner covering of the ovarian cyst. The secreting or transparent involucra are quite distinct. The *cortex ovi* is almost wholly absorbed, as it ought to be at such an advanced period. The fœtus is perfect." In the explanation of the plates mention is made of "fragments of the corpus luteum which surrounded the ovum, and was broken to pieces by the enlargement of the fœtus. Some of these fragments adhere to the inside of the ovarian coats, others are among the placental cotyledons." No account is given of the ligament of the ovary, nor of such a dissection of the parts having been undertaken as would satisfactorily prove that the sac containing the fœtus was not a cyst attached to the ovary. But the evidence in favour of ovarian gestation consists chiefly in this, that the fœtus-bearing cyst occupied the region of the ovary, and was independent of the Fallopian tube. Nevertheless this case constitutes the nearest approach to the form of gestation which it claims to represent with which I am acquainted.

In the same work (Graphic Illustrations †) is contained a description and representation of a second case termed "ovum fœcundum in receptaculo ovarico." "Through a transversal aperture in the left ovarium are seen the remains of some membranes, three in number at the least, lining a cavity which measures transversely one inch and a quarter, and about an inch vertically." The preparation belonged to Sir C. M. Clarke, who assured Dr. Granville "that a small embryo hung pendulous

* Phil. Trans. 1820, and Graphic Illustrations of Abortion, Plates X, A, and B.

† P. 27. pl. viii.

from the yet visible rudiment of an umbilical cord. That embryo, however, is not now to be seen." The female from whom this was taken was unmarried, but acknowledged herself to be pregnant. The uterus was larger than in the unimpregnated state. The Fallopian tube was not in the least involved in the enlargement. The fimbriæ were free.

A case which, in the opinion of Dr. Campbell *, "in so far as anatomical accuracy is concerned, ought to satisfy those who are still sceptical regarding the reality of ovarian gestation," is recorded in the Transactions of the College of Physicians.† From the description and drawing which accompanies it the following chief particulars are learned. The uterus, from a woman aged 30 who had committed suicide, was larger than the ungravid organ ; its body somewhat globular ; its substance, except the cervix, spongy. A decidua nearly ½″ thick, soft, pulpy, and of yellowish-white appearance, lined the interior of the uterine body. The cervix was filled with gelatinous matter, but not sealed up. The vessels of the broad ligament and appendages were remarkably distended ; on the posterior part of the left ovary, which was considerably larger than the right, was a round prominence distinct from the general fulness. The tunics of the ovary at this point were numerously furnished with tortuous blood-vessels ; and from careful examination it was clear that there had not been any aperture in the external membrane ; its surface was perfectly smooth. On dividing the membrane which covered this prominence, a distinct cyst was exposed, which contained an ovum. The internal surface of this cyst was smooth and polished, its external firmly adherent to the substance of the ovary. The ovum was simply in contact with the cyst in two-thirds of its circumference ; in the remaining third it was united to it so closely as to be inseparable. The chorion and amnion were perfectly distinct, and by the aid of a magnifying glass, vessels filled with blood were seen ramifying on the former. A yellowish honey-like matter filled the amnion, but the embryo could not be distinguished. Around the ovum for some distance the ovary was loaded with blood effused into its substance.

Except for the statement regarding the decidua there is nothing in this account which would be considered significant of pregnancy at the present time when a more perfect knowledge has been obtained of the various conditions of the ovary in health and disease. Changing the names employed to designate the cysts, this description would apply either to a follicle preparing to burst ‡, or to an incipient stage of cyst formation. To the latter it approximates more nearly. The smooth and polished inner surface of the containing cyst ; the union, "so close as to be inseparable," of the cyst termed the ovum by a third of its base to the larger one ; the presence of a honey-like matter filling this inner cyst, which is represented in the engraving as not larger than a pea, and the vessels ramifying on the cyst wall, are all conditions commonly observed in early stages of the morbid follicle.

On the other hand, the following are among the conditions which oppose the conclusion, that the ovary was in this case the seat of impregnation, viz., the absence of all trace of an embryo ; the so-called chorion, entirely wanting villi, which, in all known cases of the early ovum, more or less cover its surface ; the firm adhesion by a third of its circumference, at a time when the ovum naturally lies free and unattached even by any part of its little flocculent villous coat ; the impossibility of accounting for chorion-vessels, without an embryo to form them, and still more of explaining how the seminal fluid could reach the ovum through a membrane which is described as "perfectly smooth," and in which, "from careful examination, it was perfectly clear that there had not been any aperture ; " the absence of all mention or representation of any of those conditions of the walls of the ripe follicles which in an earlier part of this article have been shown to be always present in the follicle preparing for or soon after rupture, and which must have been present in some degree if this had been a Graafian vesicle containing an impregnated ovum. These together constitute insuperable objections to this case being received as one decisive of impregnation in the ovary, and justify its being regarded rather as an example of cystic formation, which, according to the engraved representation of the parts, it very accurately resembles ; notwithstanding that the description of the uterus and decidua would give a strong bias and indeed wish to receive this as a case in which impregnation had obtained, if the state of the parts found in the ovary had corresponded with what is now known to be characteristic of the structures formed in the earliest stages of pregnancy.*

* Memoir on Extra-Uterine Gestation, p. 33.

† Vol. vi. p. 414. 1820.

‡ See *anté*, p. 557.

* I am enabled to add in a note the following particulars relating to two of the four cases quoted above as examples of supposed ovarian gestation, and of which it may be remarked that neither are of recent date, the one having occurred thirty-eight years ago, and the other at least as early — at a time, therefore, when ovarian gestation had not been questioned, and the ovarian ovum in man had not yet been discovered. The preparation, described and figured by Dr. Granville as belonging to the late Sir C. M. Clarke, is now in the possession of Mr. Stone, by whose kindness a more particular examination of it has been permitted. For this purpose, the preparation was recently placed in the hands of Professor Owen, by whom it was removed from the bottle, and minutely examined under spirit. At this investigation, I was also present, together with Mr. Stone and Dr. John Clarke, and I had the opportunity of making repeated microscopic examinations of every portion of the ovarian structures. The result of the investigation showed that the structure supposed to be an impregnated ovum contained in the ovary, although it had such a general appearance as might without this examination have borne the interpretation which had been originally put upon it, was nothing else than an ordinary ova-

It is not necessary to multiply these examples, for no additional points of evidence could be produced which are not contained in the foregoing cases. They have been selected from instances related or quoted by various authors who have been strongest in their advocacy of the doctrine of a strict ovarian gestation, and they serve to exhibit the kind of evidence upon which that doctrine is founded. All the cases which have been employed to support this view* will be found on examination to belong to one or other of the following divisions: —

1. Cases of cysts without any embryo, and in which some supposed resemblance has been traced between the cyst walls and fœtal membranes, without any conclusive evidence of the presence of these structures being given.

rian cyst. The walls of the sac showed no separation into distinct membranes, and no trace whatever of the structures characteristic of either chorion, chorion-villi, amnion, or decidua could be discovered in them.

The outer surface of the cyst was so firmly adherent to the surrounding ovarian stroma that it could only be separated from it by considerable traction. The connecting medium was the common stroma of the ovary. The walls of the cyst, when portions were examined by transmitted light, exhibited the arrangement of vessels peculiar to ovarian cysts. The little slender depending fragment, supposed to be a rudimental umbilical cord, and very faithfully represented by Dr. Granville in Plate VIII. of the work quoted in the text, proved to be a narrow flap of the same cyst wall which had been left hanging from the edge of the sac where a portion had evidently been originally cut away in order more fully to display the preparation (the sharp edge left here by the knife or scissors being very distinctly seen). Upon transverse section of this little fragment, no trace of umbilical vessels could be found in it.

It should be observed that Sir Charles Clarke never published an account of this case.

The additional particulars which I am enabled to give with regard to the last of the four cases quoted in the text, and described in the Transactions of the Royal College of Physicians for 1820, are of another kind. That this preparation was formerly preserved in the anatomical museum of St. Bartholomew's Hospital, where the author of the case was also the lecturer on anatomy, can scarcely be doubted, from the description, exactly according with it, which appears in the first edition of the Catalogue drawn up by Mr. Stanley. (See Description of the Preparations contained in the Museum of St. Bartholomew's Hospital, 1831. Edited by Edward Stanley, Esq. Preparation 64, series xx. p. 27.) This preparation is no longer contained in the museum; and by those who are most likely to be informed upon the subject, it is not known to be in existence. The only clue that I can obtain as to its fate is derived from Mr. Paget, who informs me that, as a step preliminary to the formation of the new catalogue, printed in two volumes in 1846-51, the entire anatomical collection was carefully reexamined; and that those preparations which were found, upon such examination, not to bear out the descriptions given of them in the catalogue, or which did not serve to illustrate any point of interest, were put aside and condemned. There is, therefore, every probability that this preparation, which can now no longer be appealed to in support of the possibility of ovarian gestation, has been subjected to a similar ordeal to the former, and with a like result.

* A large collection is contained in the work of Dr. Campbell just cited.

2. Cases of dermoid cysts containing fat, hair, teeth, and bones, the nature and origin of which, independent of pregnancy, have been already considered.

3. Cases in which the evidence is more or less complete that a fœtus is or has been contained in a cavity of, or connected with the ovary.

Of the latter, as already stated, those alone suffice for examination in which the cyst has continued unattached to surrounding parts, and has remained unaffected by disintegrating and destructive processes. In this category would still be found, in all probability, a sufficient number of cases amply to have determined the question in dispute, if such methods of investigation had been pursued as the present state of anatomical and physiological science demands for the settlement of doubtful points; for in a considerable number of cases it is rendered evident that the fœtus is contained within a sac in some way connected with or occupying more or less the usual seat of the ovary. Here, therefore, the question is reduced to very narrow limits, Are these sacs formed within and at the expense of the proper ovarian structures, or are they adventitious cysts growing externally to, although connected with these structures?* If strictly within the ovary, and formed of it or of its parts, then ovarian gestation in the strict sense obtains. But this has not yet been anatomically demonstrated in such a manner as to set all objections at rest; for neither have the blood-vessels been injected in order to ascertain their new relations and distribution, nor have the tissues been microscopically examined, without which examination it would be hardly possible to determine of what parts the fœtus-bearing sac is composed. Nor have the exact limits of the serous and albuginean coats, nor the relations of the sac to the remaining ovarian tissues, nor the precise mode of connection of the fœtal membranes with the sac, been accurately traced. Nor has the condition of the yellow or corpus luteum coat of the follicle, of which brief mention only is made in one instance, been carefully examined; yet this is a point of the greatest interest and importance, because, if true ovarian gestation ever occurs, then the yellow ovisac would become the *decidua*, and the outer fibrous coat of the follicle, together with the ovarian tunics and stroma, would be the *uterus* of the ovum. But in the present state of our knowledge it cannot be said that the subject of ovarian gestation stands in any other position than that of an open question, the chief points of interest regarding which may be thus stated:—

The unimpregnated ovum is known to quit the ripe Graafian follicle by passing through an aperture spontaneously made in the walls of the follicle and of the ovary, in order to enter the Fallopian tube and uterus, in one of which canals it is afterwards impregnated.

* It is thought by Boehmer that these cases might be divided into external and internal.

It becomes a question whether this law, which has been established by ample testimony, admits of the exception that the ovum may be impregnated before quitting the follicle, and therefore whilst still contained within the ovary.

The records of various cases, in which the fœtus is apparently contained within the ovary, raise this question. For if the fœtus is found strictly contained within structures properly ovarian, then the ovum must have been impregnated within the ovary, and the seminal fluid must have entered the Graafian follicle*, for it cannot be supposed possible that the ovum, having quitted the follicle unimpregnated, should again enter it after being impregnated.

The cases, however, which have been recorded as examples of ovarian gestation do not suffice to demonstrate that the sac containing the embryo or fœtus and its membranes is strictly within the ovary, and is composed of structures strictly ovarian; and until such demonstration has been given, ovarian gestation, in the most liberal view that can be accorded to it, cannot be held to have any other signification than that of the development of the embryo or fœtus in a sac connected with or occupying the usual seat of the ovary, but not yet proved to be developed within the proper structures of that gland.

Origin of Ovarian Cysts in general. — It has been often asserted, and as frequently doubted or denied, that these cysts derive their origin from an unnatural enlargement or dilatation of Graafian follicles. Such a contrariety of views is observable equally with general pathologists, as with those who have studied the special histology of this subject. Of the latter both Rokitansky and Wedl may be considered as still holding uncertain opinions; for Rokitansky, who regards it as probable that the simple cysts are in many cases developed from the follicles, doubts that such is their origin in those instances in which their number far exceeds the usual number of Graafian vesicles, holding them to be new formations; and Wedl says that of the cysts in the parenchyma of the ovary no direct proof has ever been given that they originate in the Graafian follicles; and with respect to those which contain hair and teeth, he regards their origin in this way as "extremely doubtful."

It is obvious that a question of this kind cannot be definitively settled except by minute examination of the morbid cyst in all the early stages of its growth; an examination for which opportunities cannot very frequently arise. The choice lies between the classing of such cysts with those, on the one hand, which originate in the dilatation of natural sacculi and ducts, or with such as have their commencement in the enlarging of areolar spaces, or in the growth of primary cells or nuclei into cysts.

In the case of the ovary, it happens that the settlement of this question is more difficult than in that of most other organs; for with regard to the formation of cysts upon the latter plans, whether the views of Wedl be adopted, that they consist in an excessive augmentation of volume of the areolæ of the areolar tissue, or those of Rokitansky, that a cyst proceeds from an elementary granule which grows, by intus-susception, into a nucleus, and this into a structureless vesicle, in both views such cysts come to be composed ultimately of a cell-wall compounded of fibrous tissue and lined by epithelium — a structure which is, in fact, identical in composition with the Graafian vesicle itself.

With regard to any doubts as to the origin of cysts in Graafian follicles, which may be founded upon their number exceeding the average number of healthy follicles in an ovary, it need only be observed that the latter have been shown by the microscope to be innumerable; and with respect to secondary cysts, springing from the walls of primary ones, numerous observations prove that the impulse to cystic formation once given in an organ, even by the primitive enlargement of normal cavities, a marked tendency to the antogenous formation of cysts follows.* But even if no other explanation could be offered, the discovery of Barry, that the walls of a Graafian follicle in a natural state often contain numerous follicles of a second order, would sufficiently demonstrate the capacity of these for secondary cell-growth.

In giving the preference to that view which regards the cystic diseases of the ovary as originating in a dilatation of the Graafian vesicles, I have been guided chiefly by the following considerations.

In those cases where I have been able to discover cysts in the ovary in a stage of early formation, these have not been of less size than the average dimensions of the developed Graafian follicle.

They occur intermixed with healthy follicles, and exhibit with them the same histological formation; their tissues being altered sometimes only in such slight degrees as still to admit of their common origin with the Graafian follicle being shown.

There is sometimes exhibited in the same ovary, or in the ovaries of both sides together, a sufficient number of grades of enlargement to constitute a series of cysts, evidently composed of similar parts and tissues in various stages of growth.

Beginning with the smaller cysts, still contained in part or entirely within the ovary, there may be traced cysts of precisely similar formation and structure in every gradation of size up to those examples in which the ovary itself comes to be a mere appendage of the

* There is nothing in this supposition incompatible with the known facts relative to the spontaneous opening of the follicle, and the power of penetration of the spermatozoa occasionally as far as the distal extremity of the oviduct, or even to the surface of the ovary.

* Lebert, loc. cit. p. 244.

cyst, or in which the tissues of the healthy organ are entirely expanded and lost in the walls of the sac.

And lastly, the occurrence of these cystic formations is limited to that period of life when the Graafian follicle is in a state of activity. They are not found as new formations after the usual time at which the follicles have ceased to be discoverable in the ovaries as natural structures, nor do they occur before the period of puberty has arrived, except in cases much more rare than those of an unusually early development of these follicles, or of precocious puberty.

These arguments apply more particularly to cysts with fluid contents. How far they may also serve to explain those which contain more highly organised products is less obvious. But it must still be remembered that cystic formations of all kinds occur far more frequently in the ovary than in any other part, whilst there is nothing peculiar in the stroma of the ovary, or that portion which is external to the follicles, which would render it more peculiarly liable to cystic formations arising out of dilated areolar spaces, than similar fibrous structures occurring in other portions of the body where cysts occur.

Solid Enlargements of the Ovary. — These consist of formations of fibrous, and occasionally of imperfect cartilaginous tissues, and of osseous concretions, but more frequently of cancerous growths, formed at the expense of, or deposited within, the tissues of the ovary.

Of formations of *fibrous* tissue some account has been already given in the description of the growth of cysts. The new formations of fibrous tissue which take place in the ovary occur chiefly in the cystic parietes, where they are deposited for the purpose of strengthening the walls and enabling them to resist the increasing weight and pressure of their growing contents. But as fibroid tumours, or solid growths of the entire ovary, such formations, except those of very small size, are certainly rare, unless they are of a cancerous or cancroid nature.

It is probable, indeed, that, excepting the cancerous and cancroid cases, most, if not all, of the specimens which have been described or preserved in museums as examples of *large* fibrous tumours of the ovary, have been formed at the expense of the proper tissue of the uterus, and have had nothing to do originally with the ovary, although the latter may be so involved in the mass that its proper tissues can no longer be distinctly traced.

Such I had no difficulty in determining to be the case with a specimen preserved in King's College Museum as an example of fibrous tumour of both ovaries; each supposed ovary being of the size of an ostrich's egg, and presenting all the characteristics of the ordinary fibrous tumour of the uterus. It was rendered evident, by dissecting the parts and opening the uterus, which had not been done previously, that these large tumours which hung on either side of the uterine body had been formed at the expense of the latter, for the natural tissues of the fundus and corpus uteri were in great part absorbed into and had evidently contributed to form these masses; and out of the apex of one of these sprang the uterine end of the Fallopian tube; a clear proof that this was not an ovary.

In this way may be explained the remark of Cruveilhier, that fibrous tumours of the ovary are so perfectly identical with those found in the uterus, that it is sometimes impossible to determine to which of the organs they have originally belonged; and also the remark of Dr Baillie, that they resemble in texture the tumours which grow from the outside of the uterus. The absence of the muscular element from the natural tissues of the ovary, and the now well-known fact that the uterine fibrous tumours contain, as one of their characteristic constituents, more or less abundantly the smooth or organic muscular fibre of the uterus, forbid the belief that tumours of similar composition to those found in the uterus can be formed within or at the expense of the proper tissues of the ovary.

Cartilaginous and Osseous Formations, especially the latter, are not rare in the ovary. They are found chiefly in the parietes of cysts, and also intermixed with cancerous deposits. The process of deposition of earthy matter, which should be termed calcification rather than ossification, occurs here under three principal forms.

In fine sections of the more solid structures, or in the thin walls of cysts which are slender enough to be examined without cutting, may be often seen, with a moderate amplifying power, little aggregations of crystals in the form of clavate spicula, clustered round a centre, and forming groups scattered through a fibrous basis. Such tissues are sensibly rough to the finger, and grate under the knife.

In the second form the same calcareous materials, consisting of phosphate and carbonate of lime, combined with a small proportion of animal matter, occur as plates or laminæ, strengthening the walls of cysts; or in the shape of grains, or larger aggregations, or layers intermixed with the tissues of more solid tumours.

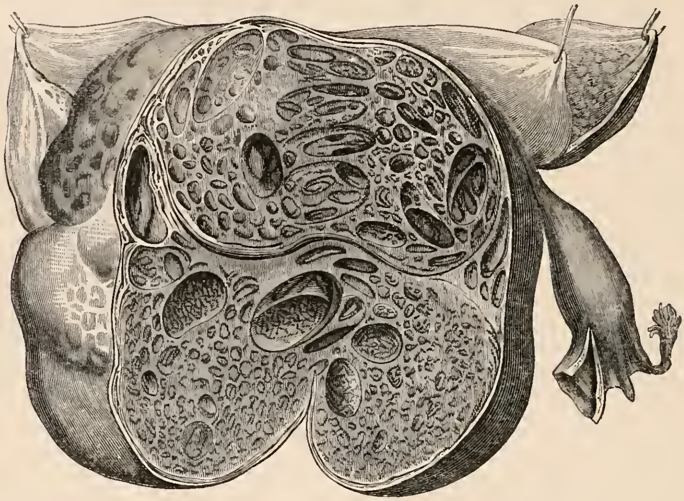
In a third form the calcareous matter may constitute an oval or solid mass contained within a small cyst, and resulting apparently from an entire calcification of the inner walls of the cyst.

The condition under which true bony structures are found in the ovary has been already considered in another section. (*See* Dermoid Cysts.)

Cancer of the Ovary occurs under the three principal varieties of Colloid, Medullary, and Scirrhous or hard cancer. Most of the large tumours of the ovary, and such of the encysted class as remain still to be described, belong to the variety of

Colloid or Alveolar Cancer, generally associated with Cysts.—These might have been classed, as has been done by Rokitansky and Lebert*, with the other forms of cystic disease of the ovary, on account of the frequency with which this form of cancer is found associated with ovarian cysts, especially of the larger class. But such an arrangement, whilst recognising an important feature, often, but not always, observed in colloid cancers of the ovary, of necessity dissociates these cases from other congeneric forms of disease. In this particular respect colloid cancer appears to stand between the various cystic diseases already described, and those forms of cancer which are not colloid, in the position of one of those "osculent groups" which have been sometimes employed in classifications of the animal kingdom as connecting links, to bring into juxtaposition objects which, though exhibiting certain near affinities, could not be included in one common group, without violence to the principles upon which a natural arrangement should be based.

Fig. 398.



Colloid cancer of the ovary. (*After Cruveilhier.*)

Not, however, to enter further upon the disputed question of the nature of alveolar cancer of the ovary, it will suffice to notice those peculiarities which are generally to be observed when the disease affects that organ.

Since colloid cancer of the ovary does not generally destroy life until the disease has made great progress, the specimens of ovaries so affected which come under our notice are often of large size, filling the pelvis and abdomen, and equalling in bulk the masses of cyst formation of a more innocent type. Such a mass, when incised, may be found to include the entire ovarian structure, which is converted into a collection of cysts, or alveolar cavities, varying greatly in size and in the thickness of their walls. Such a variety is often seen in different portions of the same structure. The surface of a section may present in some parts the appearance of a fine sponge, the alveolar spaces being condensed and somewhat flattened, in consequence of the profusion with which the alveoli have been developed. In other portions of the same tumour, and occasionally as it were in separate lobules of it, the alveoli are more expanded, and take a round or oval form, assuming the condition of distinct cysts, some of which may considerably exceed the rest in magnitude. These larger cysts may occupy a seat within the mass, or project from its surface; and probably in this way arise those still larger cystic formations in which one or more large sacs occur, having connected with them masses of alveolar structure such as those just described.

The interstitial substance, which constitutes also the boundary walls of the alveoli and follicles, is composed of a white, shining, fibrous tissue, upon the density of which chiefly depends the general hardness or softness of the mass. This intermediate substance is in some instances so thick that the cysts appear like excavations in a dense medium, but often the cyst walls are so thin that the peripheral follicles project in the form of thin-walled sacs from the surface, and the whole mass is sometimes so feebly supported as to assume the appearance of a trembling jelly. The thin-walled cysts are generally richly supplied with blood-vessels.

These cysts are filled with a viscid mucous-like material, resembling half-liquid jelly, which is sometimes colourless, but oftener of a grayish amber, yellow-green, or reddish hue. Im-

* Rokitansky, however, regards these cases as decidedly cancerous; while Lebert asserts that they have nothing in common with colloid cancer except the gelatinous contents of the cells.

bedded in the jelly-like substance may be found opaque white masses resembling blanc-mange or thick cream. Intermixed with these contents, in varying proportions, are found nucleated epithelial cells, oval corpuscles, oil granules and molecules, and delicate filaments.

Besides these contents of the alveoli, there may be often observed hanging into their interior, and sprouting from their walls, clusters of leaf-like clavate or villous processes, such as are observed in that variety which has more particularly received the name of villous cancer.

But it frequently happens that the alveolar type of structure is not generally diffused through the mass. This may form only a small portion of the diseased ovary, whilst the greater part is composed of one or more large cysts, with contents similar to those just described.

Within such cysts, or growing from the walls of those which present no other type of malignant structure, may be observed round or oval bosses, bearing no inapt resemblance to the uterine cotyledons of the cow, and exhibiting in section the compact areolar texture characteristic of the closer forms of alveolar cancer.

Colloid or alveolar cancer is occasionally found associated with medullary disease in the same ovary, whilst its presence there may be accompanied by other varieties of carcinoma in other organs, and attended by a well-marked constitutional cachexia.

Medullary Cancer of the ovary is of less frequent occurrence than the preceding variety, but like it is also occasionally associated with the formation of cysts.

Medullary cancer may occur either in the form of a general infiltration of the entire ovary with encephaloid matter, or in that of distinct tumours, bounded by a fibrous envelope, and having the carcinomatous matter distributed through an interior cellular substance, or confined there by cellular septa. These tumours may attain the size of an orange or more. Their growth appears to be in the first instance repressed by their fibrous sheaths, but these occasionally burst and allow of the diffusion of their contents. This form of cancer often affects both ovaries together, and is found associated with cancer in other and especially adjacent parts. Notwithstanding the number and variety of the contiguous structures which may be thus involved, the ovary may sometimes be traced as the centre or focus from which the cancerous deposit has spread. This was remarkably the case in an example of medullary cancer, which was for some months under my notice, where the disease commenced apparently in the left ovary, and was found to have spread from this point upwards along the chain of absorbent glands on the corresponding side, as far as the pancreas, and outwardly through the ischiatic notch to the glutæi, and all the adjacent muscles, including in its destructive march the os innominatum, which could be cut with a knife like cartilage. A medullary tumour the size of a walnut was found in the fundus of the uterus, but the rest of that organ, as well as the opposite ovary, had escaped the general destruction.

The *melanoid* variety of medullary cancer is occasionally observed in the ovary. (Roy. Coll. of Surg., No. 2642. and A.) It differs only from the foregoing in having pigment cells, of a black or brown colour, scattered through the carcinomatous matter.

Scirrhous or Hard Cancer and *Cancroid* are by no means so common as the two former varieties. Yet it is not rarely that one meets with the ovary, of one or both sides, in a hard white nodulated condition, resembling somewhat the human kidney, both in size and shape, and having its entire tissue converted into a form of cancroid, characterised by the development of a peculiar kind of stiff close-set fibres, containing between their meshes numerous nuclei (Fibro-nucleated cancroid). Such a condition of the ovary is sometimes found associated with hard cancer in other parts of the body.*

Of *Scrofulous Tubercle* in the ovary I can give no account. Most authors who refer to the subject mention it as rare, but give no decisive instances. Boivin and Dugès, however, have figured an example (*fig.* 16. Atlas) occurring in a girl of 16, associated with tuberculous disease of the mucous membrane of the uterus. In cases of my own, which I had regarded as examples of scrofulous ovary, until submitted to the microscope, I could find no trace of tuberculous matter. By Rokitansky the existence of tubercle in the ovary is altogether denied.

THE PAROVARIUM.

Syn. *Corpus Conicum. Neben-Eierstock. Organ of Rosenmüller.*

These names have been applied at various times to an organ which has hitherto received little attention, but which is nevertheless invariably present in close proximity to the ovary. The first discovery of this body is due to Rosenmüller †, who termed it the corpus conicum. It has since come under the notice of many observers, and particularly of J. Müller. And it has recently been re-examined, and very accurately described by Kobelt ‡, in an essay devoted to this subject, in which the author expresses his surprise that a structure so easily distinguished both by sight and touch, should have attracted comparatively so little attention up to the present time.

The Parovarium is most readily found by holding up the broad ligament between the observer and the light. Within the folds of this membrane, at the part where the layer

* For an example see Roy. Coll. of Surg. prep. 2636.

† Quædam de Ovariis Embryonum et Fœtuum humanorum. Leipsiæ, 1802.

‡ Der Neben-Eierstock des Weibes. Heidelberg. 1847.

of peritoneum, after investing the Fallopian tube, passes off towards the ovary, to form the posterior duplicature which encloses the vessels proceeding to that organ, will be found a small plexus of white tortuous tubes, (*fig.* 403. *a*, *b*, *c*) arranged somewhat in the form of a cone whose apex is directed towards the hilum of the ovary *l*, and its base *a c a* towards the Fallopian tube *h*. The entire organ measures about one inch in breadth, and is composed of 12—20 tubules 0·15—0·2‴ in diameter.

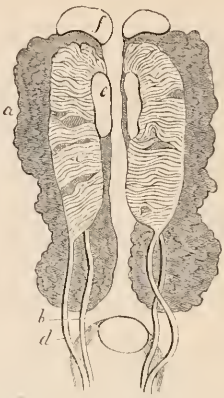
The tubes which contain nothing but a clear fluid consist of fibrous membrane, lined by a single layer of pale, cylindrical, epithelial cells. These tubular canals are not known to have any direct communication with the ovary.

That the parovarium is formed out of the Wolffian body does not now appear to admit of doubt. It has been usually considered that the Wolffian bodies are organs peculiar to fœtal life, and that they afterwards entirely disappear in both sexes. Hence no special investigations have been undertaken with a view to ascertain their ultimate fate. Meckel indeed compared them to the epididymis. Rathke believed that they became epididymis in the male, and disappeared in the female; while Rosenmüller, who discovered the parovarium, compared this body to the epididymis. Some general conjectures also have pointed in the male sex to the *vascula aberrantia* of the epididymis, and in the female to the organ of Rosenmüller and the ducts of Gärtner, as the supposed remains of the Wolffian body. Nevertheless it is, according to Kobelt, an undoubted anatomical fact that each pretended ephemeral structure not only exists through the whole of life in both sexes, but that it absolutely increases up to its highest state of perfection, and first suffers a gradual retrogression, after the extinction of the reproductive function, but never entirely disappears.

The signification and true homologies of this singular organ cannot be understood without first briefly examining the mode of formation and development of the Wolffian body, and tracing its relation to the generative gland and Fallopian tube. In this examination it is also of consequence to compare the progressive steps of formation of those parts with the corresponding structures in the male.

The Wolffian body is most readily examined in the chick, (*figs.* 399, 400.) Here during the third day of incubation are formed two canals which extend along the sides of the vertebral column, from the heart to the posterior extremity of the body. To the inner side of each canal is attached a series of blind pouches (*fig.* 399. *c* and 400. *b*), which during the next two days become lengthened and convoluted. These together constitute the Wolffian body. Behind them, and formed independently at a somewhat later period, lie the kidneys (*fig.* 399. and 400. *a*) and suprarenal bodies, (*fig.* 399. *f*, 400. *d*) and as these increase, the Wolffian bodies diminish. The testes (*fig.* 399. *e*) and ovaria (*fig.* 400. *c*) are developed upon the inner border, and in front of the corpora Wolffiana.

Fig. 399.

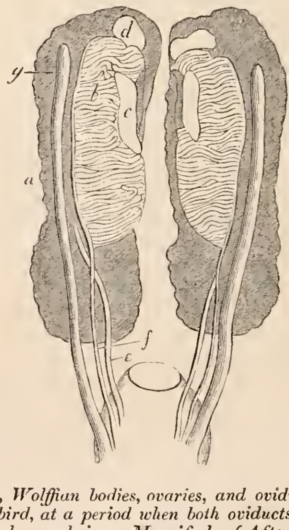


Kidneys, Wolffian bodies, and testes of an embryo bird. Magnified. (After Müller.)

a, kidney; *b*, ureter; *c*, Wolffian body; *d*, excretory duct of the latter, which, according to the views of Müller and Kobelt, afterwards becomes the vas deferens; *e*, generative gland, afterwards becoming testes; *f*, supra-renal capsules.

In the female chick, according to Müller, there is always seen an oviduct (*fig.* 400. *g*),

Fig. 400.



Kidneys, Wolffian bodies, ovaries, and oviducts of a fœtal bird, at a period when both oviducts are still of nearly equal size. Magnified. (After Müller.)

a, kidney; *b*, Wolffian body, *c*, ovary, the right * rather the smaller; *d*, supra-renal capsule; *f*, excretory duct of the Wolffian body, which in the female becomes obliterated, but in the male is converted into vas deferens; *g*, duct of Müller, afterwards oviduct or Fallopian tube.

* The drawing has been reversed in engraving. The left, therefore, should be here the right side.

distinct from the duct of the Wolffian body (*fig.* 400. *f*). In the male, however, he has been able to detect no vas deferens distinct from the excretory duct of the corpus Wolffianum; but on the contrary, the testis and the excretory duct of the former body seem to become connected by means of vasa efferentia. This is an important point, because it will be found so far to bear out the views of Kobelt regarding the homologies of these structures.

In the mammalia generally, and in man, the Wolffian bodies are less extended. They, however, possess the same arrangement of transverse cæcal tubes (*fig.* 401. *a—d*), terminating in the side of a common excretory duct (*e*), which leads from the lower extremity of the organ to the uro-genital sinus.

These structures are all formed independently of the kidneys and supra-renal capsules, as well as of the ovaria and testes, which parts occupy the same relative position in mammalia as in birds.

But here, according to Müller's researches, a different arrangement is observed in regard to the efferent duct of the generative portion of these structures. At first the oviduct and the vas deferens have each the same conformation, and each terminates by a free extremity. This, in the female, merely acquires an open mouth, and thus the Fallopian tube is formed, the ovary continuing, as at first, distinct and separate. But in the male the efferent tube and the testis become connected by transverse vessels, which are afterwards converted into the coni vasculosi of the epididymis, whilst the rest of that organ is composed of the convolutions of the efferent tube itself. "The Wolffian bodies entirely disappear in both sexes, and are not converted into any other organ." *

These views, however, leave unexplained many peculiarities which are observable in the permanent condition of the parts or organs developed from the fœtal structures; and it is the great merit of Kobelt's researches that they serve to render these intelligible.

According to this observer, there exists, in the earliest periods of intra-uterine life, a condition of indistinction of sex in every individual. This depends upon a temporary co-existence in each individual of all the elements of the reproductive structures. For at the highest point of sexual indifference, that is, shortly before the beginning of the division of sex, the Wolffian bodies consist of —

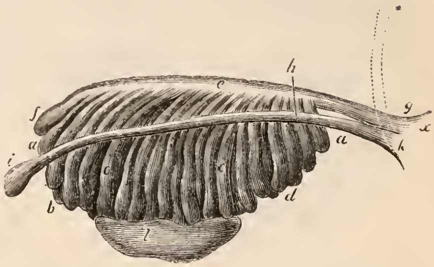
1. The so-called cæcal tubes (*fig.* 401. *a—d*).

2. Of the common duct (*e*) running along the outer side of this body, into which the cæcal tubes open.

3. And of a second longer cord (*h*), which begins in a blind pouch (*i*), and takes its course inwards over the Wolffian body, parallel with the excretory duct of the latter (*e*), in order to enter the uro-genital canal (*x*), by a separate orifice (*k*). This last cord, discovered by John Müller, is throughout destitute of any connection with the cæcal pouches. (See also *fig.* 400. *g*.)

* Müller's Physiology, by Baly, p. 1637.

Fig. 401.



The left Wolffian body at the period of indistinction of sex. (*After Kobelt.*)

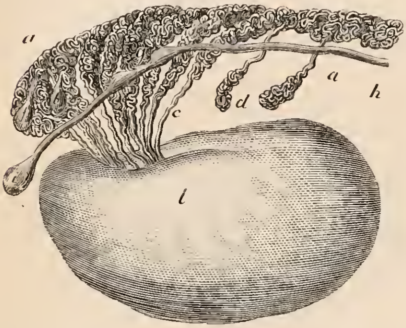
a a, entire collection of its component tubules divisible into three sets, viz., *b*, upper; *c*, middle; *d*, lower set; *e*, excretory duct of the Wolffian body into which all the tubules open, subsequently converted into vas deferens in the male, and becoming atrophied in the female; *f*, terminal bulb of the same, becoming afterwards the so-called hydatid, often seen attached, in the male, to the head of the epididymis (*fig.* 402. *f*), and in the female to the broad ligament (*fig.* 403. *f* and 408. *g*); *g*, opening of the Wolffian body into *x*, the uro-genital canal; *h*, duct of Müller, afterwards Fallopian tube in the female, and becoming atrophied in the male; *i*, terminal bulb of the same, becoming the hydatid of Morgagni (*fig.* 402. *i*) in the male, and the hydatid often seen depending from the mouth of the Fallopian tube in the female (*Fig.* 403. *i* and 368. *ee*); *k*, junction of the duct of Müller with the uro-genital canal; * shows the subsequent horizontal position of this duct when it has become Fallopian tube.

The organ destined for the preparation of the reproductive material, the generative gland, (*fig.* 401. *l*), consists of a longish, clearly defined structure, lying upon the inner side of the Wolffian body, so as to cover a portion of the bulbs of the cæcal pouches. Its white colour serves to distinguish it, at a glance, from the yellowish brown Wolffian body. As yet, no material nor actual distinction of sex can be discovered in any one of these parts; and yet the whole already contains all the elements of the male, as well as of the female, reproductive apparatus, without any true exhibition of bi-sexuality.

The nature of the first impulse towards a division of sex, in one or other direction, is unknown, but the subsequent separation manifests itself with the commencing distinctive development, and correlative retrogression of each several element; for the cardinal organ, the generative gland (*fig.* 401. *l*), may be converted into testis (*fig.* 402. *l*), or ovary (*fig.* 403. *l*), and through the doubly existing excretory duct of this gland, viz. the duct of Müller (*fig.* 401. *h*), for the female, and the excretory duct of the Wolffian body (*fig.* 401, *e*) for the male, the capability of conversion into either sex exists at this time in every individual.

The division of sex begins to be anatomically discoverable by the development of one,

Fig. 402.



Adult testis and epididymis, anterior view. (*After Kobelt.*)

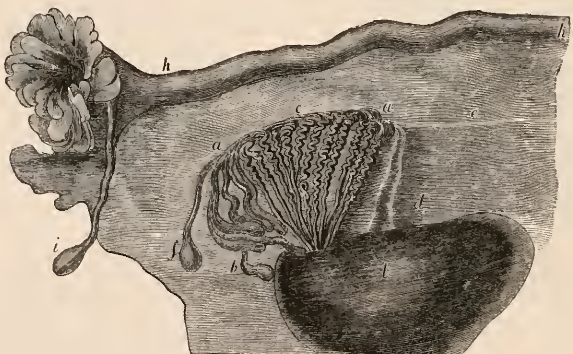
a a, entire series of metamorphosed tubules of the original Wolffian body; *b*, remains of the upper set, converted into the hydatid in the head of the epididymis; *c*, the middle set converted into the coni vasculosi; *d*, the lower set converted into the vasa aberrantia; *e*, excretory duct of the Wolffian body, now the canal of the epididymis and vas deferens; *f*, bulb of the same, now a so-called hydatid; *h*, duct of Müller, not destined to be developed in the male; *i*, terminal bulb of the same, now the hydatid of Morgagni; *g*, hydatiform swellings of the same in the border of the epididymis; *l*, generative gland, now testis.

and the stationary condition or disappearance of the other of these ducts. From this point, therefore, the course which each of these organs takes, is different for either sex. The male Wolffian body never disappears in all its parts, but is converted into the epididymis in such a manner that the middle line of cæcal tubes (*fig.* 401. *c c*) is transformed into the 18—20 coni vasculosi (*fig.* 402. *c*); while their straight and open ends, as vasa efferentia, establish a communication with the rete vasculosum testis. The upper blind pouches (*fig.* 401. *a*, *b*) and the bulb (*f*) of the excretory duct disappear, or become converted into the hydatids (*fig.* 402. *b*, *f*) upon the head of the epididymis, while the inferior pouches (*fig.* 401. *d*) disappear in part, and in part become elongated and tortuous, without forming any connection with the testis. These constitute the hitherto enigmatical vasa aberrantia of Haller (*fig.* 402. *d*).

The excretory duct of the Wolffian body (*fig.* 401. *e*) is converted into the canal of the epididymis, (*fig.* 402. *e*), and ultimately into the vas deferens, and whilst the retrogression and final obliteration of the terminal part of this duct takes place normally in the female, (*fig.* 403. *e*) it constitutes a pathological condition when it occurs in the male. The terminal bulb (*fig.* 401. *i*) of the duct of Müller is converted into the hydatid of Morgagni (*fig.* 402. *i*), whilst its inferior portion (*fig.* 401. *h*) still exists, at a later period in the anterior border of the epididymis (*fig.* 402. *h*).

Tracing the development of the corresponding structures from the same point of departure as in the male, we find that in the female, also, the Wolffian body never disappears entirely, but is employed in the formation of the parovarium. Its middle blind

Fig. 403.



Adult parovarium, ovary, and Fallopian tube. (*After Kobelt.*)

a a, entire series of tubules of the original Wolffian body; *b*, remains of the upper set, which occasionally become distended by collections of fluid, and constitute one form of dropsy of the broad ligament; *c*, middle set of tubules forming the principal part of the parovarium; *d*, lower set atrophied, answering to the vasa aberrantia in the male; *e*, atrophied remains of the excretory duct of the Wolffian body; *f*, terminal bulb of the same, converted here into the hydatid often seen attached to the broad ligament; *h*, the former duct of Müller, now Fallopian tube, with its infundibulum, from which hangs *i*, the terminal bulb, now converted into a pedunculated hydatid; *l*, generative gland, now the ovary.

These three last figures are from Kobelt, whose views they illustrate. The letters refer to corresponding parts in each.

pouches (*fig.* 401. *c c*), are converted into the 18—20 tubules of the parovarium (*fig.* 403. *c*), and these secerning tubes become organically connected with the hilum of the ovary, *l*. They are the homotypes of the male coni vasculosi, and vasa efferentia, but which constitute here vasa adferentia.

The superior blind pouches and the bulb of the excretory duct disappear, or contribute to form the hydatids at the outer border of the parovarium (*fig.* 403. *f b*), which are so commonly mistaken for morbid structures.

The inferior blind pouches (*fig.* 401. *d*) remain and represent the vasa aberrantia of Haller (*fig.* 402. *d*), in the male. Several of them become elongated and intermingled with the vessels of the spermatic plexus (*fig.* 403. *d*).

The excretory duct of the Wolffian body (*fig.* 401. *e*) in the female, undergoes a retrogression in its whole length, and the lower end disappears entirely. (*Fig.* 403. *e*).

The duct of Müller (*fig.* 401, *h*) is converted into the Fallopian tube (*fig.* 403. *h*), and its bulb (*fig.* 401. *i*) becomes the terminal hydatid of the same (*fig.* 403. *i*). This latter structure, of which a very excellent example, as occurring on both sides, is given in *fig.* 368. *e e*, is very constantly present in the adult. Like the so-called hydatid (*fig.* 403. *f* and 408. *g*) at the outer border of the parovarium, it is frequently mistaken for a morbid product, and is often so designated in descriptions of these parts; an error which the improper title of hydatid tends to propagate.

The interruption or deficiency of the Fallopian tube in the female is a malformation, which represents a normal condition in the male.

The parovarium exhibits parallel stages of development and retrogression with its corresponding ovary at different periods of life.

Abnormal Anatomy of the Parovarium. — So little attention has been given to this structure in its natural condition that accurate information regarding its morbid states can hardly be looked for. The so-called hydatids, which are found at the outer border of the parovarium in most adult specimens, and which are constructed out of the superior blind pouches and bulb of the excretory duct of the Wolffian body, have been already just noticed as normal structures. These are found pretty constantly in younger subjects, while the hydatids of later formation in the alæ vespertilionum are formed of the remains of the canals of the retrograde parovarium. Within the walls of these canals is collected occasionally a considerable amount of fluid, and it is probable that this is the origin of those larger accumulations to which the term dropsy of the broad ligament has been applied.

FALLOPIAN TUBE OR OVIDUCT.

Normal Anatomy.

Tubæ uteri vel Fallopianæ; oviducti; vasa spermatica vel ejaculantia, Lat.; *Muttertrompeten*, Germ.; *Trompes utérines, Trompes de Fallope*, Fr.

The Fallopian tube (*fig.* 368. *c c*, and 404. *a b c*) is the excretory duct of the ovary, as its homotype, the vas deferens, is the excretory conduit of the testis. And while in an anatomical point of view the tube is an appendage of the uterus, in a physiological sense it must be regarded as the proper appurtenance of the ovary. But the Fallopian tube differs from the vas deferens, as well as from every other excretory duct in the animal economy, in this important particular, that it is entirely detached from its proper gland, between which and the uterus it serves to establish only a temporary communication.

This separation of the oviduct from the ovary is associated with a higher type of general structure than that which accompanies the blending of these parts. It is first observed in the cartilaginous fishes, and prevails in all classes of the animal kingdom above them; while in the osseous fishes and in the invertebrata possessing distinct ovaries, the oviducts are directly continuous with those bodies.

The Fallopian tube or oviduct is developed equally on both sides of the body in all vertebrate animals, except in the class Aves, where the right tube becomes atrophied at an early period, while the left alone is developed.

In the human subject each ovary is provided with its proper oviduct, which serves to convey the ova from either side to the central organ, the uterus. But the detached position of the oviduct permits so great a range of motion in its free extremity, that, not only can this be applied to every part of the surface of the corresponding ovary, but the tube of one side may occasionally serve as a conduit to the opposite gland, and receive its product. The action of the tube, however, is then imperfect; and, when impregnation obtains, an abnormal form of gestation usually results.

Form and dimensions. — Each oviduct has the form of a conical tube, the base of which is free and directed towards the ovary, while its apex is attached to the corresponding superior angle of the uterus, out of which it appears to arise.

The form of the tube was compared by Fallopius to that of a horn or trumpet, which instrument, when straightened or only slightly curved, it sufficiently resembles. Issuing from the upper angle of the uterus, at the point of junction of the superior and lateral borders, the oviduct commences round and narrow (*fig.* 404. *c*), and proceeds outwardly gradually and regularly widening up to its distal extremity, where it contracts somewhat suddenly just before terminating in a widely expanded funnel-shaped orifice. In the latter half of its course the tube exhibits certain flexuosities, which produce an appearance of contraction at intervals. But that no such contractions really exist is rendered evident by

Fig. 404.

Left Fallopian tube from an adult. (*After Richard.*)

a, pavilion and fimbriæ; *b*, body of the tube; *c*, abdominal orifice; *d*, tubo-ovarian ligament and fringes; *e*, commencement of the tube; *f f*, tubal mesentery; *g*, ovary; *h*, ligament of the ovary; *i*, uterus; *l*, round ligament.

distending the tube with air or water; a process which invariably removes this appearance, and serves to demonstrate the uniform and equable enlargement of the canal.

The length of the tube varies in different subjects, and to a slight extent on the two sides of the same subject. But this difference is not nearly so marked as that often observed between the respective distances of the two ovaries from the uterus. The ordinary range of length of the tube, measured between its extreme points and disregarding the flexuosities, is $3\frac{1}{2}$—$4\frac{1}{2}''$; but the curvature and flexuosities add usually 1—$1\frac{1}{2}''$ to this length.

The breadth of the tube is considerably greater at the distal than at the proximal end. Just at the point of emergence from the uterine border, where the tube is firm and cord-like (*fig.* 404. *e*), its external diameter is $1\frac{1}{2}$—$2'''$. From this point it gradually increases in breadth, and becomes softer, so as to assume the general appearance of an intestine. The mean diameter of the tube is found at about three-fifths of its length (*b*) from the uterine end, where it measures $2\frac{1}{2}'''$; from this point the enlargement is more rapid, until the greatest diameter is attained just before the terminal contraction occurs, and here the transverse measurement is $5'''$.

Situation and connections. — Of the three structures termed appendages which arise in a triangular form from the superior angle of the uterus, the Fallopian tube occupies the apex of the triangle, while, at nearly equal distances from it are inserted the ligament of the ovary, and the round ligament; the former posteriorly, and the latter anteriorly. In the natural position of the parts, the tube, viewed from without, appears to spring from the uterine angle with a slight downward curve (*fig.* 404. *e*), and then inclining horizontally forwards and outwards, it describes an irregular semicircle, whose inner side looks backwards towards the ovary (*g*), which is placed nearly opposite to the centre of its length (*figs.* 368. and 404.). Such at least are the relative situations which these parts exhibit when spread out equidistantly from each other: although it is probable that during life they are more collapsed and lie closer together, — the anterior wall of the tube then being in apposition with the sides and back of the bladder, while its posterior wall corresponds, at its centre, with the ovary, the superior border with the small intestine, and the inferior with the fold of peritoneum by which the tube is attached to the broad ligament. The mouth or abdominal end of the tube is generally directed inwards and backwards, towards the distal extremity of the ovary, in close proximity to which it is preserved by means of the tubo-ovarian ligament (*figs.* 368. *n* and 404. *d*).

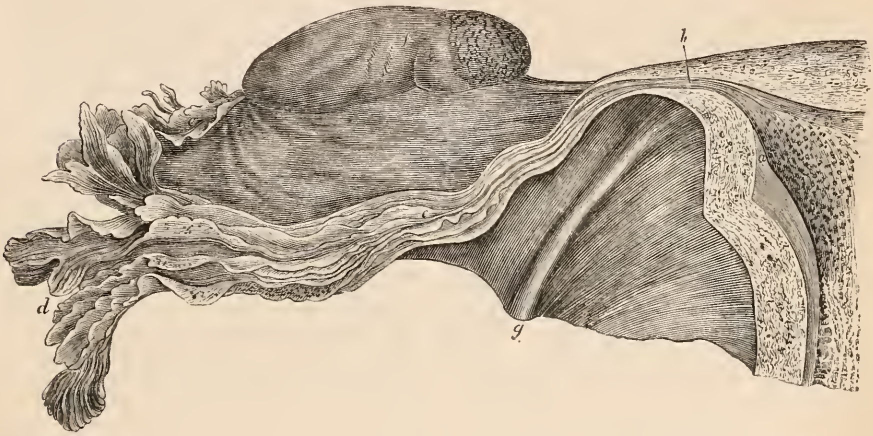
The fold of peritoneum (*fig.* 404. *f*), which connects the tube with the main portion of the broad ligament resembles a mesentery and serves to convey blood-vessels and nerves, as well as to sustain the tube in its place, and to limit its movements. It constitutes that portion of the broad ligament termed the middle wing. The Fallopian tube occupies the entire upper border of this wing, and receives from it a complete peritoneal investment, except along the lower border or line of junction of the two surfaces of membrane composing it, at which line the vessels and nerves enter. Thus the tube resembles an intestine in the mode of its investment, but with this difference, that the peritoneal coat is more loosely applied, especially in young subjects; where the convolutions of the tube are more distinctly marked, and lie free within the sheath, which does not follow their windings (*fig.* 418.).*

The tubal mesentery (*fig.* 404. *f*) is triangular, or somewhat falciform in shape. Its narrow pointed end is directed towards the uterus, where the tube has scarcely any capacity for independent motion; but as the depth of the mesentery increases outwardly greater freedom of movement is permitted. The greatest breadth of the mesentery is found at a distance of two thirds of its length from the uterine extremity, and here it measures $1\frac{1}{2}''$. From this point a slight narrowing occurs, and the membrane terminates in an abrupt margin $1\frac{1}{4}''$ in length, which extends from the lower border of the mouth of the tube to the bulbous extremity of the ovary.

This border, which is thickened by the addition of a layer of mucous membrane derived from the mouth of the Fallopian tube, constitutes the tubo-ovarian ligament (*fig.* 404. *d*).

Separate parts and divisions. — The full extent of the Fallopian tube cannot be ascertained until the entire canal, in its interior, has been laid open. The tube which, externally viewed, appears to spring from the

Fig. 405.



Right Fallopian tube laid open. From an adult who had not borne children. (After Richard.)

a, funnel-shaped canal leading from the uterus to *b*, uterine portion of the tube; *c*, point at which the large plicæ commence; *d*, infundibulum covered by plicæ, continuous with those lining the canal; *e*, tubo-ovarian ligament and fringes; *f*, ovary; *g*, round ligament.

superior angle of the uterus, is thus seen to commence by a small orifice, *ostium uterinum*, upon the inner surface of the uterus. This orifice conducts to a narrow canal (*figs.* 405. *b* and 406.) which, after traversing the walls of the organ, and constituting the *pars uterina*, expands into a gradually widening tube (*fig.* 405. *c*), whose form nearly corresponds with the external configuration of the part. Towards the extremity of this canal, a sudden contraction occurs, constituting the external orifice of the tube, *ostium abdominale* (*fig.* 404. *c*). But this does not form the termination of the oviduct, for the latter immediately widens into the trumpet-like orifice (*infundibulum*), whose margin, split up into numerous fringed processes, (*fimbriæ*), (*fig.* 404. *a a*) give to that part the torn and jagged appearance suggestive of the idea that it has been bitten or torn, as expressed in the name, *morsus diaboli*, applied by ancient writers to this part. Each of these parts exhibit peculiarities of structure, requiring a special description.

Internal, or uterine orifice, ostium uterinum. — This orifice, which ought to be regarded as marking the termination rather than the commencement of the tube, is found at the extremity of a short, funnel-shaped conduit, (*fig.* 405. *a*) which leads from the general cavity of the uterus into the upper and outer angle on either side of that organ. Here, while there is no abrupt line of demarcation to indicate the point of commencement of the canal, the characteristic structure of the uterine mucous membrane gradually ceases. The peculiar arrangement of its capillary vessels and the orifices of the uterine glands,

* For a further account of the reflections of peritoneum, which enclose the uterine appendages see "Ligaments of the Uterus," in this article.

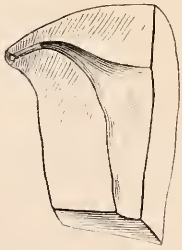
can no longer be discerned, and a slightly plaited condition of the lining membrane of the canal begins to be distinguishable (*fig.* 405. *b*).

At this precise point is found the true uterine orifice of the canal, the diameter of which varies in different subjects, but is rarely of larger size than suffices for the easy passage of a common bristle. The true diameter of the tubal cavity at this point is best exhibited by a transverse section; for when the canal is laid open longitudinally, and its walls are separated as at *b*, in *fig.* 405. this portion of the interior of the tube appears to have a greater diameter than it actually possesses when the parts are closed, and in a natural state. In some subjects, however, and in certain conditions of the tube, the uterine orifice may be sufficiently patulous to admit of the passage of a fine probe.

Uterine portion of the tube, pars uterina. — This, as just stated, is the portion of the oviduct which traverses and is included in the substance of the uterine walls. Its length will vary, in some degree, with the varying thickness of those walls, in different subjects; yet not entirely so, because this canal does not pierce the uterine parietes in a direction perpendicular to their surface, but traverses them in an oblique manner, while the tissues become gradually attenuated around it, in a direction from within outwards (*fig.* 405. *b*).

But the course of the tube through the uterine walls may be still more satisfactorily traced by the aid of a section made down to, but not laying open, the canal. The peculiar white colour of the tube is thus made to contrast strongly with the surrounding darker uterine tissue; and this peculiarity is rendered more striking when a fine injection of the part has been made. The canal of the tube may thus be readily traced from its infundibular-shaped commencement running, in the first half of its course, in a direction obliquely upwards and outwards, and in its remaining half, either horizontally outwards,

Fig. 406.



Entrance of the Fallopian tube into the uterine cavity, dissected down to the mucous membrane, which is left unopened. (*Ad Nat.*)

or more commonly turning rather suddenly downwards, and forming, with its first direction, an angle of 60° (*fig.* 406. and 431.).

Strictly, the Fallopian tube should be deemed to commence at this point; and this should be regarded as the true *ostium uterinum*, while the short infundibular canal leading to it from the uterine cavity should be considered a portion of that cavity, representing, in fact, the cornu of the uterus in mammalia. The peculiar form of this portion of the tube is not without interest, for it appears to me to offer a probable explanation of the occasional detention of the impregnated ovum, in its passage through this division of the oviduct, where its development produces the variety of extra-uterine pregnancy termed by Breschet interstitial.

Canal of the body of the tube. — While the portion of the Fallopian tube already described, as contained within the substance of uterine walls, is rightly termed its uterine or fixed portion, the main part, which is external to them, constitutes the free portion. This also is traversed in its entire length by a canal, the form of which corresponds generally with that of the tube itself. It is occupied by numerous longitudinal folds of the lining membrane (*fig.* 405. *c*), which are so closely placed as to convert the channel of the tube into a series of minute capillary canals. These folds never disappear by distension like the folds and furrows upon many mucous surfaces, such as the œsophagus, bladder, &c.; but they are true plications, like the valvulæ conniventes of the small intestine, as pointed out by M. Richard, who has very accurately described their arrangement.* Each of these is composed of two layers of mucous membrane united together by cellular tissue. Their direction is constantly parallel with the axis of the tube. In the uterine region of the oviduct, they constitute two or three small projecting and rigid crests, forming the little capillary channels, but in proportion as they advance towards the outer part, they become more elevated and numerous, and at 2 or 3 fingers' breadth from the uterus commence the large floating folds which are prolonged as far as the pavilion. These floating plaits are from 4 to 6 in number; they acquire a breadth of 2—3‴, and are themselves covered by an infinite number of little crests, often imbricated the one upon the other, and intercepting between them little capillary canals. On a level with the abdominal opening these large folds cease, the small ones only remaining; but still one of these large folds always extends beyond the orifice.

External orifice, ostium abdominale. — This occupies the bottom of the funnel-shaped expansion or trumpet-like end of the oviduct, and is formed simply by a constriction of the tubal walls at a short distance from the irregularly notched margin in which they terminate. The aperture is fringed in its entire circumference by the plications of the membrane already described (*fig.* 405.). These radiating towards the centre appear nearly to obstruct the entrance of the tube,

* Thèse, p. 35.

which, however, during the middle period of life is usually of sufficient capacity to admit easily of the introduction of a moderate-sized catheter. The constriction which forms this aperture is not occasioned by any thickening nor other alteration of texture in the walls of the tube, so that after the parts have been laid open, it is often difficult to determine the exact seat of the previously existing orifice by any mark except that of a slight diminution in breadth of the walls at this spot.

The Pavilion, or Infundibulum consists of the expanded or trumpet-mouthed portion of the tube which lies between the orifice just described and the fringed margin in which the tube-walls actually terminate. No portion of the Fallopian tube is so variable in form and construction as this, and yet none is of such importance, for upon the peculiar construction of this part depends the special action of the oviduct in grasping the surface of the ovary, and receiving and conveying away the ovum.

The representations which in illustrated works usually accompany the description of this part serve to give but a feeble notion of the beauty of its construction, apparently because the advice of De Graaf, that their structure should be examined under water, has been commonly neglected. But without the support derived from a fluid of greater density than the atmosphere, the extremely delicate plicæ and fringes with which the expanded mouthpiece of the tube is beset, collapse and exhibit nothing more than a general indication or outline of their true form.

When thus examined, the pavilion in young and healthy subjects is observed to be funnel-shaped, and to have arranged upon its inner surface numerous folds and leaflets, which are merely continuations of the larger and smaller plicæ lining the cavity of the tube. These folds, which are irregularly though often very closely set, converge towards the centre of the orifice of the tube, and in some cases appear by their profusion almost to block up the entrance of the canal. The office of these folds is doubtless to receive and entangle the delicate ovum in one of the numerous channels which are formed between the sets of leaflets, and so to conduct it infallibly into the common orifice towards which they all converge.

So great is the variety perceptible in the conformation of this structure in different subjects, that it would be difficult to find any two in which a precisely similar arrangement of parts obtained. Even in the same body there is often a material difference in the pavilion of the two sides. And these varieties are not attributable to mere individual peculiarities of form, but they appear to bear a certain relation to the age of the person in whom they are found*, and consequently to the period of functional activity or otherwise of the structures of which they form an importart part. Thus in young subjects, after the age of puberty, and in those who have borne few children, the pavilion exhibits that richness and profusion of folds and fringes which is represented in *figs*. 404. and 419. while in multiparæ and those advanced in life a greater simplicity of form in this part is commonly observed ; but between these extremes every variety of arrangement may be observed.

In the fœtus, and in very young subjects, the margin of the pavilion is nearly evenly circular. This form is also seen in adults in those rare cases where the prolongation of one of the fimbriæ along the tubo-ovarian

Fig. 407.

Portion of Fallopian tube from an adult. (After Richard.)

a, external surface of the fimbriæ; *b*, line of demarcation between the mucous and serous membranes; *c c*, body of the tube; *d d*, tubo-ovarian ligament, presenting scarcely any trace of the fringes.

ligament does not occur, but commonly the margin is uneven or scolloped, as shown in *fig*. 407.

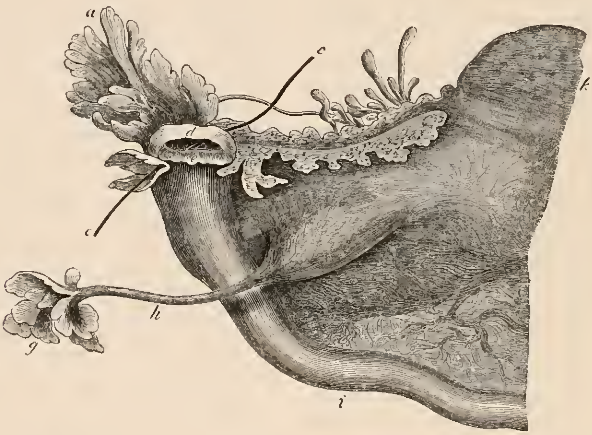
At this point, the opportunity occurs of examining an arrange ment of parts which is unique in the animal economy, viz., the conjunction of a serous with a mucous membrane. The line of junction of these two

* Richard, Thèse, Anatomie des Trompes de l'Utérus chez la Femme. 1851.

surfaces may here be traced along the margin where the tube wall terminates. Here the peritoneal or outer covering of the tube may be observed to cease suddenly in the form of a distinct boundary line, as in the example represented in *fig.* 407. But occasionally the peritoneal coat is prolonged upon the base of the principal leaflets which crest the end of the canal, and in that case a closer examination is necessary in order to discover the line of union between the mucous and the serous surfaces.

The fimbriæ, laciniæ (λακίς), *or morsus diaboli.* —The structure and composition of these appendages differ in no respect from those of the plicæ or folds of which they are merely continuations. These fimbriæ present many varieties of form, but are generally either petiolate, lanceolate, or simply filiform. Their margins are in some cases coarsely crenate, like those of the tubal plicæ, while in other instances they are so finely indented, as to require the use of a lens for their examination. The greater number of these fimbriæ are attached to the sides or margins of the infundibulum by their narrower extremity only, like leaves thickly clustered on the branches of a tree, while the more obtuse extremity of each leaflet is left free, apparently with the object of increasing the extent of surface of the tube-mouth, which may be applied to the superficies of the ovary. But very commonly one or two fimbriæ are observed to be firmly attached by both ends, while the body extends horizontally in the form of a flattened band among the rest of the fringes, as at *fig.* 408. *d.* The backs of these are always covered by a continuation

Fig. 408.



Abdominal end of right Fallopian tube, from an adult. (*After Richard.*)

a, fimbriæ irregularly formed; *c c*, bristle passed through an accessory pavilion; *d*, horizontal band across the mouth of the tube formed by one of the fimbriæ having both ends fixed; *g h*, peduncle ending in fringed processes, probably the terminal portion of the Wolffian duct. (See *fig.* 401. *f*, and explanation.) *i*, body of Fallopian tube; *k*, ovary. The tubo-ovarian ligament and fringes are well developed in this specimen.

of the serous membrane. It is difficult to imagine a use for them unless they are placed there as a safeguard to diminish the risk of a retrograde movement and escape of the ovum after it has entered the tube along one of the furrows formed between the plicæ.

The length of the fimbriæ ranges from $\frac{1}{2}'''$ to $\frac{3}{4}''$. The principal leaflets, being continuations of the 4 — 6 main plicæ of the tube, exceed the rest in size, and these, spreading like rays, form the more salient points of the fringes, while the intermediate spaces are filled up by the smaller appendages.

Intermixed with the latter are often seen minute pedunculated cysts, and especially little white hard grains, the size of millet seeds, first noticed by De Graaf. Similar grains are often observed upon the mesentery of the tube, or attached to the outer surface of the tube itself (*fig.* 404.).

The Tubo-ovarian ligament and fringes. — This so-called ligament (*fig.* 408.) consists of one of the fimbriæ, which is almost constantly prolonged upon the outer margin or base of the triangular mesentery of the tube. Extending in the form of a slight furrow or channel (*fig.* 404. *d* and *fig.* 405. *e*), between the outer extremity of the ovary and the inner or lower border of the tube, it is margined on either side by a row of leaflets, possessing shapes as variable as those which characterise the rest of the lesser fringes. These leaflets, as well as the furrow between them, are backed by a continuation of the peritoneal fold or mesentery, which, after enclosing the tube, here terminates abruptly on a level with its mouth, and thus is produced the appearance of a ligament, whose use is simply to preserve the tubal orifice in contiguity to the ovary; but there is no reason to think that it performs, as the ancient anatomists supposed, the office of a muscle in drawing these parts together.

The length of the tubo-ovarian ligament determines the distance to which the mouth of the tube can be separated from its corresponding ovary. This, in most instances, is sufficient to permit the tubal orifice to be easily applied over any portion of the gland of the same side; so that from whatever part of the surface of the ovary an ovum is discharged, the reception of the latter by the tube is rendered possible by the range of motion which the mouth of the tube enjoys in relation to the ovary. The average length of this ligament, measured from its commencement at the margin of the ovary to the centre of the tubal orifice is $1\frac{1}{2}''$.

Structure of the coats or tunics. — The Fallopian tube is composed of three coats: — viz., 1. an external investment of peritoneum; 2. a proper coat composed of fibrous tissue; and 3. a mucous lining covered by epithelium.

The tube has been already described as running horizontally within two folds of peritoneum, formed by the upper border of the lesser wing, or ala of the broad ligament, which serves also to form its mesentery, and to connect it with adjacent parts. This fold encircles the tube somewhat loosely, and constitutes the peritoneal coat.

Between this covering and the middle or proper fibrous coat of the tube is found a small quantity of fine and rather tough connective tissue, which serves to bind these coats together. This intermediate tissue being more abundant in quantity towards the uterine end, permits a greater freedom of movement of the serous investment of the tube in this region than at the opposite or free extremity, where, in most subjects, the serous and proper coats cannot be separated without much difficulty.

The middle or fibrous coat has been very generally regarded as containing muscular fibres, and as having a contractile power. Santorini described external, longitudinal, and internal circular fibres, and his statement has been reasserted by Meckel, Boivin, Velpeau, and many others. By Kölliker, also, the middle layer of this tube is regarded as a smooth muscular coat, composed of a double layer of fibres. These statements have been called in question by Robin and Richard, who assert that there are in the proper walls of the oviduct only fibres of cellular tissue and fibro-plastic elements, but no muscular fibres of organic life. M. Richard declares that it is impossible to recognise two distinct layers, at least they can be only artificially produced. The number of longitudinal fasciculi appears always to exceed that of the transverse fibres, but these elements are interlaced in every direction, both longitudinally and transversely.

The question is important, for unless we consider, with Haller, that the proper tissue of the tube resembles the cavernous body of the penis and clitoris, and that, as some have supposed, the tube, when filled with blood, is capable of erection, for which conjecture there appears to be no good foundation, it is impossible, in the absence of a contractile fibrous coat, to explain those movements of the oviduct, which must necessarily occur whenever the abdominal orifice is applied to the surface of the ovary — or that peristaltic action of the tube, witnessed by Bischoff in the Guinea-pig, by means of which the ova are carried backwards and forwards within the canal. See p. 611.

With a view of resolving the doubts raised by these conflicting statements, I have microscopically examined the fibrous coat of the oviduct in the human subject at different periods of life, as well as in several genera of mammalia, and especially in Simia, Bos, Cervus, and Delphinus. With regard to these latter examples, I find the evidence of the presence of a smooth muscular layer, constituting the middle coat of the oviduct, more or less decisive in different genera, but the existence of such a coat was most satisfactorily determined in Delphinus phocæna (pregnant). Here not only were the smooth muscular fibres, collected into long bundles, easily distinguished, but they were still more distinctly shown at the broken extremities of the latter, which exhibited the characteristic fusiform terminations of the individual fibre in such a manner as to leave no doubt as to the muscular nature of the tissue forming the principal portion of this coat, which contained besides an abundance of nuclear elements and common fibres of connective tissue.

With regard to the human subject, it appears to me that the assertion that the middle coat of the oviduct contains only fibrous tissue, may have been based upon the examination of specimens taken from females advanced in life; for, applied to such specimens, the statement is generally true, but in younger subjects, and when the proper reagents have been used, I have experienced no difficulty in finding more or less satisfactory evidence of the presence of smooth muscular fibres, provided only that a sufficiently high power, and the mode of illumination suitable to the discrimination of such tissues, were employed.

It must be observed, however, that the condition of this tissue is very variable. In some subjects, the greater portion appears to consist of nuclear elements which here and there are seen intermixed with fusiform fibres of greater or less length. In other instances, the tissue is more distinctly fibrillar, the fibres being collected in bundles consisting of flattened filaments with distinct fusiform terminations intermixed with bundles of white fibrous tissue; while in some, and, I believe, generally in older subjects, the latter form of fibre, as just stated, abounds, and appears to constitute the principal portion of the middle coat of the tube.

The arrangement of the fibres constituting this coat is chiefly in the direction of the axis of the tube. This, indeed, appears to be entirely so at the surface; but deeper towards the central canal, numerous flat bundles crossing the former at right angles are encountered, and these become more abundant still nearer to the mucous membrane, although, so far as I have been able to trace them, they do not constitute so distinct and separate a layer as the outer longitudinal stratum.

The general condition of the lining membrane of the tube, and its peculiar arrangement, having been already described, it is only needful here to explain the composition and texture of this coat. This membrane, although commonly regarded as a mucous membrane, contains neither discoverable glands nor villi. It is composed of a very delicate pink or white soft layer, consisting of undeveloped connective tissue, mixed with numerous fusiform formative cells.

This thin layer is united to the fibrous coat by a small quantity of submucous tissue, which is also found lying between the folds of membrane forming the plicæ, or ridges, and serving to connect together the two layers of which they are composed.

Covering this coat upon its inner surface is a thin layer of long cylindrical epithelial cells of a form peculiar to the Fallopian tube, of which Henle has given a minute account.* These, which are conical or filiform, are furnished with an oval flattened nucleus, and have at their broad, unattached end a distinct row of cilia. These cells may be traced through the entire length of the tube, from the uterus to the free border of the fimbriæ, where they gradually diminish in size, and, at the point of junction with the peritoneum, acquire the flattened form of the cells of pavement epithelium.

Under ordinary circumstances, and when the organs are healthy, the canal of the Fallopian tube contains only a small quantity of slightly viscid mucus. But when death has taken place during a menstrual period, the fluid is found to be replaced by blood which is usually of a dark colour, and uncoagulated. This fluid presents, under the microscope, the characters of ordinary blood, with which numerous epithelial scales, derived from the walls of the containing tube, are intermixed.

Blood vessels and nerves. — M. Richard is, so far as I am aware, the only author who has been at the pains to examine and describe with anything like minuteness the precise arrangement and distribution of the blood-vessels supplying the Fallopian tube. The following is his account, the general accuracy of which I have verified by frequent injections of these vessels.

"There exists always a special artery for the tube. Springing from one of the numerous branches of the uterine artery, near the angle of the uterus, this vessel takes a direction from within outwards, from the commencement of the oviduct, as far as the neighbourhood of the pavilion, describing, like the tube itself, a curve, the concavity of which looks towards the side of the ovary. The artery, which is lodged in the substance of the mesentery of the tube, takes a slightly sinuous course, parallel with the oviduct, and at the distance of one or two finger breadths from it. Situated in the middle of the filamentous cellular tissue, which exists between the two layers of peritoneum, it passes constantly behind the organ of Rosenmüller; so constantly, that keeping this relation in mind, one could immediately, if the neighbouring organs were removed, distinguish the anterior from the posterior face of the lesser wing of the broad ligament. The artery is accompanied by the two veins of the tube, and surrounded by very delicate nervous filaments.

"The branches furnished by this artery are lateral as well as terminal. The lateral branches are generally three in number. The first enters the inner third of the body of the tube, at a distance of three or four centimetres from the uterus; the second supplies the middle, and the third the outermost extremity of the oviduct. These three branches before arriving at the tube bifurcate, the twigs resulting from which bifurcations are directed the one to the right and the other to the left to inosculate with each other. From this results a series of arches furnishing branches to every portion of the body of the tube. The innermost bifurcating branch anastomoses with a branch derived from the proper artery of the uterus, so that a well-marked analogy between the distribution of the tubal artery and that of the mesentery is here observable. The terminal division is distributed to the pavilion. It separates into a greater or less number of tortuous branches, each of which goes to supply a fringe of the pavilion; the tubo-ovarian fringes also receive each a twig of the tubal artery. Sometimes, however, a small branch of the utero-ovarian artery, from which it is detached opposite to the external extremity of the ovary, establishes one of the anastomoses between the uterine and the utero-ovarian vessel. From the concavity of the tubal artery very small branches proceed to the organ of Rosenmüller, and to the neighbouring cellular tissue."

But no adequate notion can be formed of the extreme richness of supply of vessels to this and the neighbouring organs until, after a successful minute injection, the parts have been dried and preserved in balsam. Numerous vessels which the opacity of the parts had previously concealed are then brought into view. They are seen running parallel with the surface of the tube, and mostly converging towards the fimbriæ, upon and in the substance of which they lie as thickly as the pile of velvet, previously to their dispersion into their final capillary terminations. It was probably this exuberance of vascular supply that led some former observers to imagine that the tube possessed an erectile tissue, a structure of which the most minute injections do not suffice to exhibit a trace.

The veins, which follow the same course

* Encyclop. Anat. Gen. t. i.

as the arteries of the tube, frequently anastomose with one another by transverse branches, which serve to connect together the two principal trunks. These gather the returning blood and carry it into the plexus of uterine veins placed along the sides of the uterus.

The lymphatics of the tube have the same common source as those supplying the rest of the internal generative organ.

The nerves, which are very slender, follow the course of the arteries. They are derived, according to Dr. Snow Beck, from the hypogastric and aortic plexuses.

FUNCTIONS OF THE FALLOPIAN TUBE.

It has long been determined, with as much precision as the nature of the subject apparently admits, that the Fallopian tube performs the double office of receiving the ova from the ovary, and conveying them into the uterus, and of receiving the spermatic fluid from the uterus and conveying it in the direction of the ovary: the tube itself being, if not constantly, at least generally, the seat of impregnation; or, in other words, the precise spot in which the material contact of the male and female generative elements takes place.

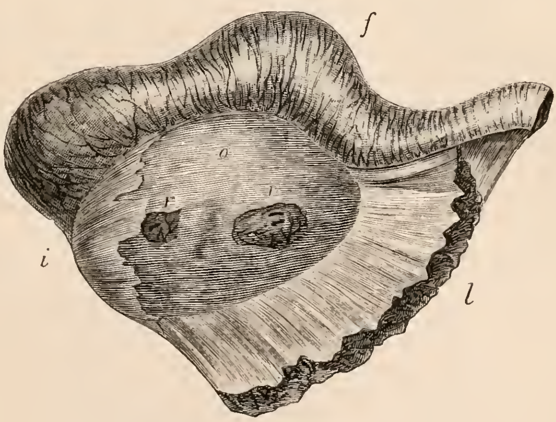
These conclusions regarding the offices of the oviduct, are deducible from various observations and experiments, both of a positive and negative kind, made upon mammalian animals, and the close correspondence which has been observed between these and similar observations, so far as they can be made upon the human female, leads also to the conclusion that there is little or no material difference between the mode in which these offices are performed in man and in the mammalia generally.

With regard to the demonstrative evidence furnished by experiments and observations upon animals, as well as by observations upon the human subject, relative to the precise offices of the oviduct in the conveyance of the ova from the ovary, the following points may be considered as established.

The infundibular orifice of the Fallopian tube, together with the fimbriæ by which its margin is fringed, at the time of the discharge of ova, becomes expanded over a certain portion of the ovary, the extent of the surface covered varying according to the form and proportions of the infundibulum relatively to the size of the ovary.

In some mammalia, the cat for example, the infundibulum is sufficiently large to encompass the entire ovary, so that an ovum escaping from any portion of its surface would fall within the receptacle thus provided for it, and be conveyed to the orifice of the tube, and thence into its canal. But in many animals of this class, as well as in man, the size of the infundibulum does not suffice to cover more than a portion of the ovary at any one time, half or a third it may be of the entire surface of the gland; so that in all these cases a selection must be made of the exact spot from which the discharge of an ovum is about to take place, or else the ovum would be lost, by falling into the cavity of the abdomen. That this occasionally happens is rendered evident by those cases in which the infundibulum is glued as it were to a portion of the ovary by morbid adhesion. But while the extremity of the oviduct is thus immoveably fixed, the process of ovulation still goes on from all parts of the ovarian surface indifferently, so that those ova only which might happen to be discharged from the particular spot to which the tube is affixed, would by any possibility enter its

Fig. 409.



Ovary of a woman who died during menstruation.

The coats of the ovary are attenuated in two places. Three apertures, *r r*, two being in juxtaposition, lead to as many Graafian vesicles from which ova have been recently discharged, escaping apparently into the cavity of the abdomen. The infundibulum is glued to the extremity of the ovary by morbid adhesion. The tube is distended by accumulated fluid; *o*, ovary; *i*, infundibulum; *f*, Fallopian tube; *l*, broad ligament. (*Ad Nat.*)

mouth, and all the rest would be lost. I have already adverted at p. 560. to such an example, and of this case a drawing is here subjoined. In this instance, three ripe Graafian vesicles had burst on one side of the same ovary, and had discharged their ova, while the mouth of the corresponding oviduct was inseparably united by morbid adhesions to the outer extremity of the gland, and was thus effectually prevented from receiving any ova except such as might be discharged from the spot to which the tube was attached.

By what power the mouth of the tube is directed to the particular portion of the ovary from which an ovum is about to be discharged remains entirely unknown, as, indeed, does also, to a certain extent, the precise nature of the mechanism effecting this movement. The part termed the tubo-ovarian ligament (*fig.* 404. *d)* will at all times serve to keep the infundibulum in contiguity with the ovary, but by what agency the orifice of the tube is drawn towards, and its fimbriæ become expanded upon, the ovary, cannot be very satisfactorily explained. These movements can only be referred to the contraction of the low form of fibre of which this part has been shown to be chiefly composed ; and although it is certain that in a great many of the invertebrata, a similar form of contractile fibre constitutes the sole agency by which their active and sometimes very rapid movements are effected, yet this is not commonly found to be associated with any considerable degree of movement in the higher animals.

The temporary adhesion of the infundibulum to the surface of the ovary when an ovum is about to be discharged, appears to be effected by the interposition of a slimy mucus, which possesses sufficient tenacity to require the employment of some slight force in drawing the parts asunder, and which is furnished, probably, by those numerous minute folds or plicæ so plentifully covering this portion of the tube.

It was formerly supposed that this apposition of the mouth of the tube to the ovary occurred only under the influence of the sexual orgasm ; an inference which was natural so long as the belief remained general that the ova were discharged from the ovary only as a consequence of sexual congress. But this circumstance admits of a modified explanation, now that the discharge of the ovum in mammalia is known to occur during the "heat," or that period in which alone the coitus is permitted by the female. The apposition of the Fallopian tube to the ovary at such times is to be regarded as a movement providing for the safe passage of the ova to the uterus, and, in regard to time, as preceding the act of impregnation, although it might endure until after a fertilising coitus had taken place, and so the parts would occasionally be found in such a state of apposition in an animal killed immediately or shortly after that event ; thus appearing to warrant the conclusion that the venereal orgasm had been the cause of this movement. The mode in which the ovum is expelled from the ovary has been already described at p. 560. In the form there represented, the ovum is received into, and is conducted along, the Fallopian tube ; and, on account of the interest which attaches to the earlier developmental changes occurring here, it has, perhaps, been more frequently examined in this situation than in any other portion of the generative track. Barry's tables include the particulars of ninety-three ovula, found in various parts of the tube in the rabbit, between 10 and 70 hours post coitum. Bischoff's observations were made upon 60 or 70 ovula within the tube in the same animal, as well as upon many more in other mammalia. Several instances of the same kind have been already quoted, two of these being in the human subject; and almost every anatomical collection contains examples of the human ovum abnormally arrested and developed in the tube.

In what way the ovum, after its reception by the mouth of the tube, is conveyed along that canal into the uterus, is explained by the peculiar construction of this part. The tube being lined longitudinally by slender folds which divide it into numerous capillary canals, and having every part of its inner surface covered by cilia, vibrating, according to Henle, in a direction towards the uterus, appears admirably adapted for the conveyance of the minute ovum downwards from the place of its formation to its seat of normal development. The peculiar form of the oviduct, which is more or less funnel-shaped, especially in the human subject, further conduces to this direction of the ovum downwards, while, in many instances, its course appears to be aided by that peristaltic action of the walls of the tube which many observers have noticed, and of which a further account will be presently given.

The period of time occupied by the descent of the ovum through the tube does not usually exceed a very few days. This, however, appears to be a variable feature in different mammalia, and regarding which, even in those animals admitting of the readiest observation, it appears very difficult to arrive at definite conclusions, chiefly on account of the uncertainty belonging to the determination of the precise moment at which the ovum quits the ovary.

In the bitch the ovum, after quitting the ovary, is supposed to remain in the tube susceptible of impregnation during 6 or 8 days; and its passage is probably quite completed in 10 days. In the guinea-pig the ovum makes its passage in a much shorter time, as it usually enters the uterus at the end of the third day. In the rabbit the time is nearly the same. The ovum, surrounded by a thick layer of albumen, passes from the oviduct into the uterus at the end of the third or beginning of the fourth day. While in the roe, although the time occupied is probably longer, yet, at the most, in a few days, the ovum, unaltered in size, as in other cases where it receives no albumen in the tube, reaches the uterus, and there, if impregnation has taken place, it remains four and a half months without undergoing any positive change. In man little is known accurately respecting the time occupied by the passage of the ovum through the tube. Only two instances have been recorded in which the human ovum has been actually seen in the tube (see p. 567.), with the exception of abnormal cases.

The attempt to determine this point in the human subject has generally proceeded upon a comparison of the condition of early ova found in the uterus, or prematurely expelled from it, with the last known date of intercourse or of menstruation; but neither of these modes of calculation can afford any certain information: for it is obvious that the first can give no more than the date of insemination (as, for example, when a single intercourse has occurred), but will throw no light upon the question of the time which may have elapsed since the ovum quitted the ovary, and how long it may have remained unimpregnated in the tube; while the second mode is rendered equally uncertain for want of more precise knowledge than we at present possess of the actual relation in point of time between menstruation and ovulation. See p. 669.

The analogies which other mammalia furnish justify, to a certain extent, the supposition, that the time occupied by the passage of the ovum through the tube in man is not materially different. But the circumstance that, in man, the periods of capacity for impregnation are not restricted to definite occasions, to the same extent that they are in brutes, greatly diminishes the value of any calculations which might be based upon these analogies.

We may next examine the evidence by which it may be shown that the Fallopian tube serves, on the other hand, as a conduit for the spermatic fluid towards the ovary. That it performs this office, in addition to that of conveying the ova downwards into the uterus, is abundantly proved by the direct observations of Prevost and Dumas, Bischoff, Barry, Wagner, and many others; whose experiments serve to show, also, to what extent the spermatozoa are capable of penetrating within the tube, and of retaining their power of motion there.

Bischoff, after repeatedly finding spermatozoa in active movement in the vagina, and particularly in the Fallopian tube of the bitch, though in this latter situation the movements had ceased, was so fortunate as to trace them in an animal that had been lined on two successive days, and was killed half an hour after the last coitus, not only in the uterus, but also in active motion through the whole length of the tubes, and between the fimbriæ, and finally in the sac or capsule which the peritoneum forms around the ovary, and even upon the ovary itself. Wagner also found in a bitch, killed forty-eight hours after coitus, spermatozoa motionless in the vagina but active in the uterus, in whose cornua, as well as in the Fallopian tubes, their number and activity conspicuously increased as far as the abdominal extremity, where they completely filled every fold of membrane, and were seen moving among the fimbriæ, but none were found in the capsule or pouch that surrounds the ovary. By Barry the same fact of the possibility of the spermatozoa penetrating to the utmost extremity of the tube, and even as far as the surface of the ovary, has been demonstrated. Of the latter he gives two instances; but that the seminal fluid does not commonly penetrate so far as the ovary may be inferred from the statements of Prevost and Dumas, who could never find them in this situation, and of Barry, who, acknowledging the accuracy of those observers, says himself, that in seventeen out of nineteen instances in the rabbit, he was unable to detect the spermatic fluid upon the ovary, and in one of the two cases in which he had observed it there, the only evidence of the fact was the presence of a single spermatozoon.

By no observer, so far as I am aware, have spermatozoa ever been detected within the ovary of any mammal.

The rapidity with which the spermatic fluid is capable of reaching and entering the tube is sometimes very considerable. Bischoff has observed spermatozoa within the oviduct of the Guinea-pig immediately after the coitus; in one instance, indeed, he traced them as far as the middle of the tube, in little more than three quarters of an hour after that event, though it had been commonly supposed that a period of nine or ten hours was requisite for the penetration of spermatozoa to the extremity of the tube.

The power by which the semen reaches the oviduct is partly the act of ejaculation, which may suffice to carry it to the end of the uterus, partly the peristaltic action of the uterus and tubes, in those animals in which these parts have flexible walls; partly, also, the movements of the spermatozoa themselves. But the cilia lining the tubes can in no way contribute to this effect, since their action would create a current in the contrary direction to the ascent of the fluid.

Thus it has been shown that the Fallopian tube, or oviduct, performs the double office of conveying the ova from the ovary towards the uterus, and of serving as a conduit for the passage of the spermatic fluid from the uterus towards the ovary; and the conclusion is almost inevitable, that, by these combined operations, the encounter of the generative elements will most probably take place at some point within the tubal canal. It may, however, be objected, that since the spermatic fluid has been known occasionally to reach as far as the ovary, impregnation may occur there; or, on the other hand, that inasmuch as this fluid must necessarily, in part at least, fill the uterus before it can occupy the oviduct, the ovum may not become impregnated until after it has reached the principal cavity of the generative track.

In order, therefore, to determine as nearly as possible the precise limits of the functions of the oviducts, it will be necessary to examine more particularly the evidence, which serves to show, that while the ovary is the part in which the ovum is formed, and the uterus that in which it is developed; the Fallopian tube, besides being the conductor of the ovum from the formative to the recipient organ, is also the seat of the second most important step in the process of generation, namely, its fertilisation.

Here human physiology is so much at fault that it again becomes necessary to resort to the evidence furnished by experiments, and observations made upon the mammalia generally.

Now, one of the most remarkable circumstances relating to the generative process in the mammalia is, that the periods of separation of the ova from the ovary, and of their passage down the Fallopian tube, are coincident with the œstrus. Bischoff, indeed, has ascertained, in the bitch, that by the time the ovum has reached the uterus, or even the lower end of the oviduct, the period of heat, or desire for sexual congress, has passed away, and consequently the opportunity for impregnation is lost. In the Guinea-pig also it appears certain that the opportunity for impregnation is already gone by the time the ovum has quitted the tube, and has reached the uterus; for the œstrus is then long passed, the coitus has long ceased to be permitted, and even the vulva is at this time again contracted. And although doubtless these conditions vary in different genera, yet a variety of circumstances, of which a more particular account will be presently given, renders it probable that the rule is general among the mammalia, that insemination shall occur coincidently with the passage of the ovum down the Fallopian tube.

Next, it may be shown, by the experiments of Cruikshank, Haighton, Blundell, and Bischoff, which consisted in deligation or excision of portions of the tube, that whenever the obliteration of the canal was complete, and had been effected prior to the act of copulation, fertilisation of the ovum was rendered impossible.

These experiments were most satisfactory when performed on one side only of the generative organs, so as to leave free play for the natural functions of the other; and thus the negative results obtained on the one half of the body being set off against the positive ones of the other, served to enhance the value of both. By such experiments it may be shown that mechanical obstruction of the tube, while interfering in no respect with the spontaneous separation of the ovum from the ovary, or its reception by the mouth of the tube, and descent as far as the seat of obstruction (provided indeed that care is taken in the experiment not to destroy the vascular supply of the parts), prevents the completion of the reproductive act, and stops it at this stage, by impeding the access of the spermatic fluid to the ovum.

But the results of such experiments will necessarily vary according to the time and place of application of the ligature. Thus while division or deligation of the tube before, or even very shortly after, intercourse prevents impregnation of the ova, yet, according to Haighton, the same experiment performed sixty hours after coitus had no effect whatever in impeding the development of the embryo, for in that time the encounter of the generative elements would have already taken place.

But although these experiments may be infinitely varied, they cannot afford such satisfactory information as may be derived from the actual examination of the contents of the tube where natural impregnation has been allowed to obtain, especially when these examinations have been conducted with the aid of the microscope. In this way may be obtained an amount of collective evidence that leaves little to be desired for the purpose of fully elucidating the history of the ovum during that brief but important period which intervenes between its quitting the ovary and its entrance into the uterus. But since an account of the development of the ovum does not come within the scope of this article, only so much of the subject will be given here as will be requisite to continue the argument for the purpose of showing what is the precise part which the Fallopian tube takes in the process of impregnation.

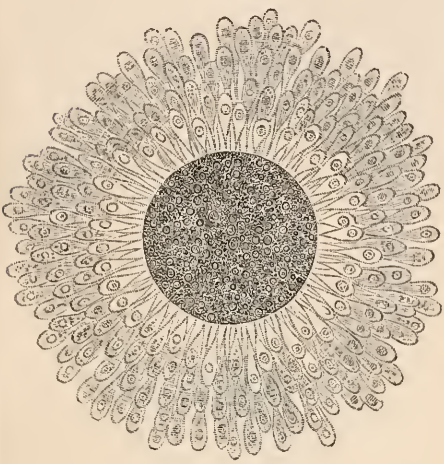
There can be no question that the mammalian ovum, after an efficient coitus, enters the uterus in a condition differing in many important particulars from that in which it ordinarily quits the ovary. And although a certain amount of variation is perceptible in regard to the actual changes experienced by the ovum in different species, during its passage through the tube, yet so constantly are the main features preserved, that the observations made upon any one species will generally serve as a type of the rest, and certainly the aggregate of these observations, agreeing closely as they do with one another, render the conclusion in the highest degree probable, that changes not very different from these occur also in the ovum in man.

Barry asserts that "there is no condition of the ovum, uniform in all respects, which can be pointed out as the particular state in which it is discharged from the ovary." Nevertheless the ripe ovum which is about to be expelled, or one which has been just discharged, presents certain well-marked characteristics, of which the following are the most important.

The ovum is closely invested by a layer of nucleated cells. These form a portion of the granular membrane or lining of the Graafian follicle in which it is imbedded, and when the ovum is discharged from the follicle, as described at p. 560., a portion of these granules is carried with it into the mouth of the Fallopian tube.

In ova which are not quite ripe, these nucleated cells are round, but during the œstrus, in the riper ova, the cells become elongated and fusiform, having their pointed ends attached to the zona pellucida or bounding membrane of the ovum. They present a glassy swollen aspect, by which the fully ripe

Fig. 410.



Ripe ovum from the ovary. Guinea-pig. (After Bischoff.)

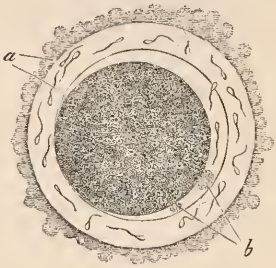
ova acquire an appearance of being surrounded by rays. This change occurs in most mammalia, as the dog, rabbit, sheep, rat, roe, and kangaroo. It is characteristic of the mature ova, and may be regarded as a certain sign of their ripeness.

Corresponding with this external alteration in the appearance of the ovum, are certain internal changes, of which the chief is the disappearance of the germinal vesicle. This indeed seems to be an almost constant phenomenon throughout the mammalia, though, as to the precise mode, or even time, of disappearance of this important constituent of the ovum, observers are by no means agreed. By Barry it was considered, after close observation, that the vesicle was not dissolved nor ruptured, as many now suppose, but that it became lost to observation by retiring to the centre of the ovum, where it was changed in character by an internal process of cell development.

These changes, external and internal, are the precursors of impregnation, and characterise the ovum shortly prior to and at the period of its quitting the ovary.

Arrived within the Fallopian tube, the first alteration which the ovum experiences is the stripping off of the ray-like appendage of nucleated cells with which it quitted the ovary. This change results apparently from a bursting and diffluence of these cells, now no longer capable of serving any useful purpose; for the conjecture that they might furnish materials for the construction of the chorion has not been supported by any direct observations. On the contrary, numerous observations of Bischoff show that this process of freeing the ovum from its surrounding layer of cells, takes place very soon after its entrance within the tube, and generally in the upper third.

Fig. 411.



The ovum on first arriving in the Fallopian tube. The ray-like appendages are nearly stripped off. (After Bischoff.)

a, zona pellucida; *b*, granular bodies between the zona pellucida and yelk. Rabbit.

And now, if the coitus does not obtain, and no contact of the generative elements occurs, the ovum perishes; observations at least relative to its further fate are wanting. But should the ovum have become fertilised, then a noticeable series of changes takes place, of which the following are the most important.

The zona pellucida, or transparent bounding membrane of the ovum, having been freed of its external granular investment, the entire ovum presents the condition represented in figure 412. Deprived now of all encumbrance, the surface of the ovum is in a condition eminently favourable for the passage through it of the spermatozoa, which penetrate readily that soft outer coat, and thus gain admission to the yelk.

The fact of the penetration of the outer coat of the ovum by the spermatozoa, which has been so often asserted and denied, may now, after much controversy, be considered as established. In the mammalian ovum, this passage may take place apparently through any portion of the outer coat, just as it does in the ova of amphibia, and not through a special pore or microphyle, such as exists in the ova of osseous fishes.

Following this act of penetration occurs a change which apparently affords the first distinct evidence that the power of the spermatozoa has been efficiently exerted upon the ovum. The yelk, which had previously completely filled the zona, is observed to have become contracted, so that an interspace is left between it and the zona, termed by Newport, who has carefully watched its formation in the ova of amphibia, the "respiratory chamber." Such a retiring of the yelk, so as to leave an interspace between the latter and the zona pellucida, which interspace is filled by a transparent fluid, has been noticed in many mammalia, as the Guinea-pig, rabbit, &c.

Fig. 412.

The ovum a little more advanced in the tube. (After Bischoff.)

The surface is perfectly smooth. Spermatozoa have penetrated the zona pellucida. The respiratory chamber is formed between the latter and the yelk. The rotation of the yelk has commenced, as indicated by the arrows. The granular bodies appear preparatory to the segmentation of the yelk. Several of these stages are seen commencing in the preceding figure. Rabbit.

This change is preliminary to another occurrence, which has been observed in the ova of many animals, both vertebrate and invertebrate, viz. the rotation of the yelk within the interspace just described; — a rotation which is effected by the aid of cilia clothing the surface of the yelk.

About this time may be observed one, or perhaps two, small granular bodies, whose formation has given rise to many and varied speculations regarding their signification and use. They occupy a portion of the space between the yelk and zona pellucida, and appear to be common to the mammalian ovum and that of other classes. The most probable supposition regarding their use connects them with the division or cleavage of the yelk which follows their appearance.

Whatever doubts may be entertained as to the dependence of the phenomena already described upon a preceding act of impregnation, all question is set at rest at this point, by the direct experiments of Newport, who

Fig. 413.

The ovum still more advanced in the tube. (After Bischoff.)

The first stage in the segmentation of the yelk has taken place. Rabbit.

ascertained beyond doubt, that segmentation of the yelk is the result of impregnation alone, and that it never takes place in the unimpregnated ovum.

This segmentation of the yelk consists in a spontaneous cleavage of that body, at first into two, and then into four, equal parts; the process of division continuing in geometric progression until the whole is broken up into a mass of finely nucleated particles, between which the original sperm-force is probably equally divided.

Segmentation of the yelk of the mammalian ovum has never been observed in its commencing stages anywhere but in the tube. The extent to which it proceeds before the ovum quits the oviduct to enter the uterus appears to vary in different species. Bischoff never saw more than four yelk-divisions in the ovum of the Guinea-pig by the time that

Fig. 414.

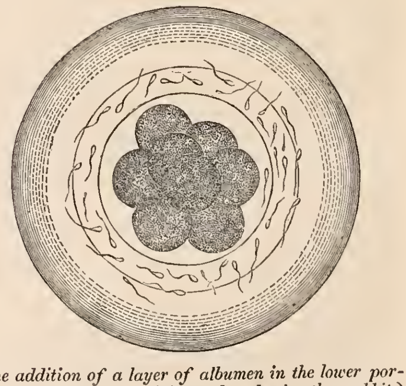
The ovum from the lower or uterine end of the Fallopian tube. (After Bischoff.)

The yelk exhibits four divisions. Rabbit.

it had reached the lower portion of the tube; and it is probable that a further division into eight parts occurs in the extreme end of the duct, since, in the next condition of the ova found in the uterus, the yelk exhibited 12—16 divisions.

The only remaining change in the condition of the ovum during its residence in the ovi-

Fig. 415.



The addition of a layer of albumen in the lower portion of the tube—(observed only in the rabbit.) (After Bischoff.)

The yelk exhibits eight divisions.

duct, which it is necessary here to notice, is the addition, sometimes, of a thick layer of albumen around the zona pellucida, which is formed upon it in the middle and lower portions of the tube. But this is certainly not a constant, and apparently not even a common occurrence. It occurs in the rabbit, but not in the bitch, Guinea-pig, or roe.

These are the principal and more obvious changes which the ovum experiences in its passage down the Fallopian tube until it enters the uterus. So regular is the order with which they succeed each other that particular portions of the tube may be assigned as the seat of each occurrence. Thus the first, or upper third of the oviduct is appropriated to the reception of the ovum, which, soon after quitting the ovary, is here deprived of its adventitious covering of nucleated cells, and is thus prepared for the full operation of the spermatozoa, whose active movements in this part of the tube have been frequently noticed. Here also spermatozoa have been frequently seen upon, and even within, the ova; and here the first changes characteristic of the commencing operations of the sperm force, such as the formation of the respiratory chamber, and rotation of the yelk, may be noticed. In the middle of the tube the ova commonly exhibit still more decided evidences of impregnation. The cleavage of the yelk has already commenced, and one or more granular bodies occupy the space between it and the zona. The ova found in the lower third, except those which may be destined to perish, always show unmistakable signs of impregnation, of which the segmentation of the yelk, now advanced to the production of 12—16 divisions, is the most expressive.

If the views of Bischoff be correct, it is in the upper third, or at farthest in the middle of the tube, that impregnation must occur, unless indeed it takes place at the ovary. For in the lower end of the tube the more definite developmental changes of the ovum occur, or otherwise the ovum perishes. In the dog and Guinea-pig, by the time the ovum has reached this spot, the œstrus is past, and the animal will no longer permit the coitus.*

Connected apparently with some of the foregoing steps in the process of generation, though it does not appear precisely with which, is a phenomenon described by Bischoff as occurring in the Guinea-pig. Several times Bischoff had the good fortune to observe with a lens, and also under the microscope, a peristaltic action in the walls of the oviduct, by which the contained ova, visible through them, were moved backwards and forwards. The ova appeared to be surrounded by a transparent fluid, in which they floated.

Now, such an observation is interesting, when viewed in connexion with two circumstances, specially observed and proved by Newport, namely, that in the artificial impregnation of the ova of amphibia, although the process of impregnation is *commenced* at the instant of contact of the spermatozoa with the ova, yet a certain duration of contact is essential to its *completion*. And further, that although an exceedingly minute quantity of spermatozoa suffices to impregnate the ovum, yet impregnation takes place more tardily when the number is extremely limited than when the number is in full abundance; while when the quantity is reduced below a certain amount, or the duration of contact is limited, then the phenomenon is incomplete, and partial impregnation, evidenced by imperfect segmentation of the yelk, and arrest of the further stages of development, is the inevitable result.

Since, then, it cannot be supposed that a less perfect or complete contact of the ova with the spermatozoa is needful to their impregnation in the higher than in the lower vertebrata, there seems to be good ground for conjecturing that this peculiar peristaltic movement in the walls of the Fallopian tube, which has been noticed also by other observers, may have for one of its objects the more perfect commingling of the two generative elements, the spermatozoa and the ova, which, proceeding as they do in opposite directions, and encountering each other in some portion of the canal, would thus be carried backwards and forwards, and thus a certain permanence of contact, such as Newport has shown to be necessary in the amphibia, would be insured to them. And this supposition may be further strengthened by the reflection that while an onward movement in either direction would serve for the conveyance of each element singly along the tube, a backward and forward motion alternating could only retard either or both processes, and that there could be only one apparent advantage in such retardation, namely, the retention of both elements for a longer or shorter time in permanence of contact.

To sum up the offices of the Fallopian tube, the following may be said to have been with certainty ascertained to belong to that division of the generative organs: To receive the spermatic fluid from the uterus and convey it upwards through the entire canal, and as far sometimes as the ovary; To receive contrariwise the unimpregnated ova, as they are discharged from the ovary, by means of its expanded open mouth, which in these cases, where the entire ovary cannot be grasped, is guided, by a process hitherto unexplained, to select and apply itself to that

* Pouchet (L'Ovulation Spontanée) places the seat of impregnation lower down in the oviduct. He asserts that it is only about the middle of the tube, or more particularly in its lower portion, and even in the cavity of the uterus itself, that the material contact of the ova with the spermatozoa can occur. And he regards the passage of the semen as far as the extremity of the tube, and its arrival at the ovary, as an "excessively rare anomaly." But these statements are based upon examinations directed only to the detection of the presence of spermatozoa in the oviduct, and are not connected with microscopic observations of those developmental changes in the ovum, which are indisputably the results of impregnation, and of which an account has been given in the text.

particular spot from which the ripe ovum is about to be expelled; to convey the ovum in a direction opposite to the course of the fertilising fluid, so as to ensure the meeting and commingling of the generative elements, an event to which the limited calibre joined to the peristaltic action of the oviduct probably in a great degree contributes; to afford protection to the ovum during that brief sojourn in which the first effects of fertilisation are manifested upon its constituent parts; to aid probably in certain changes which are operated upon the surface of the ovum, consisting first, in all cases apparently, in a stripping off of the adventitious covering with which the ovum is invested on entering the tube, and secondly, in some instances, in the addition of certain materials which increase slightly the bulk of the ovum; and lastly, in transmitting onwards the ovum, so altered and prepared for more complete development, to the cavity of the uterus, or in conveying away those which, for want of impregnation, are destined to perish.

In reference to these conclusions regarding the offices of the Fallopian tube, which the present state of physiology appears to warrant, the question here naturally arises, how far they are applicable to the female of man, or to what extent her case may be viewed as exceptional on account of certain differences in her organisation and habitudes.

One of the most observable of these differences is the absence of that marked distinction of periods alternating with each other, such as are shown in a greater or less degree in the females of most mammalia in regard to the activity of the sexual functions.

That these alternating periods of desire and aversion to the coitus are strictly significant of corresponding temporary states of physical capacity and incapacity for conception, is placed beyond doubt, by the results of examination of the internal organs and their contents at these respective periods.

In those animals in which the œstrus returns at short intervals, the male generally remains potent at all times. The temporary incapacity is on the side of the female, and occurs in the *intervals* between the successive acts of ripening and discharge of the ova from the ovary, together with their passage down the tube. It has been shown that during these events only will she receive the male, and therefore, on that account also, is conception then only possible.

This circumstance is rendered more striking in animals in whom this interval is longest, as in the roe-deer, where the œstrus returns only once annually, and in whom the capacity for procreation is limited to a few weeks, for the reason stated by Bischoff, that then the ovary contains ripe ova and the testes ripe semen, and at no other time.

But in the human female, whatever views may be entertained regarding the connexion of a separate act of ovulation with each menstrual period, it is certain that here a marked œstrus is wanting, and that although the capacity for impregnation is apparently greatest about the times of menstruation, yet, notwithstanding the assertions of those who maintain that there is a perpetual recurrence of temporary incapacity for procreation, there is no period at which the healthy human female can be shown to be positively incapable of conception during any part of menstrual life.

It may, however, be asked whether the occasional occurrence of impregnation during an intermenstrual period, at a date more distant than usual from the last menstrual act can be explained consistently with a strict interpretation of the law that menstruation and ovulation are contemporaneous acts.

This appears to be reconcilable with the circumstance that although these acts, so far as observation has yet gone, are very frequently and perhaps usually coincident, yet exceptionally an ovum may be emitted during an intermenstrual period, the *ripening* and not the time or the act of emission of the ovum being probably the essential feature, or that the ovum, supposing it to have been emitted from the ovary at the time of menstruation, may possibly remain in the tube susceptible of impregnation longer in the human female than in the mammalia generally, or may even be impregnated after reaching the uterus. *

That the Fallopian tube in the human subject is, occasionally at least, the seat of impregnation, is demonstrated by the occurrence of the tubal form of extra-uterine gestation; while the numerous examples already quoted of other mammalia render it highly probable, by analogical reasoning, that this is the *normal* seat of that function in man.

That the first encounter of the generative elements may also take place either in the uterus or upon or even within the ovary, is plainly possible. That it occurs sometimes at or near the ovary is evidenced by the varieties of extra-uterine gestation termed ovarian and ovario-tubal. It is even possible that, in some of these, insemination may have been so coincident with the spontaneous opening of the Graafian follicle, that the spermatozoa, penetrating further than usual, may have reached the ovary at that precise moment when a passage had been prepared for the ovum, and some may have actually passed into the follicle and have impregnated the ovum there. No argument certainly can be opposed to this on the ground of physical impossibility †; while, on the other hand, it is also conceivable that impregnation may be delayed until after the ovum has entered the uterus, as in the case just suggested of a fertilising coitus occurring later than usual after the menstrual period; but I am not aware of any good anatomical or physiological reason for regarding the uterus, as by pre-

* These points are more fully considered under the head "Menstruation," p. 668.

† See the argument regarding the anatomical evidence for this form of gestation at p. 586.

ference, the seat of normal impregnation; while such a view is opposed to those numerous observations upon the mammalian ovum generally, which show, that before the ovum quits the oviduct, the developmental changes in it are already advanced many stages, while, by the time that it arrives at the uterus, the opportunity for impregnation has already passed away for that occasion.

Development of the Fallopian Tube.

Whatever difference of opinion may exist regarding the origin of the excretory duct of the male generative gland, there appears to be no doubt, that in birds at least the corresponding part in the female has its commencement in a structure which, as soon as it can be recognised as a distinct tube, is altogether separate from the Wolffian body. This is called after its first observer, the duct of Müller * (*fig.* 400. *g*).

The mode of origin of this duct has been already partly described in the account which has been given of the formation of the Parovarium (p. 594.). Its development may be most conveniently traced in birds, where it can be easily shown that the oviduct is not a metamorphosis of the excretory duct of the Wolffian body, but may be distinguished lying near it, in the form of a tolerably thick tube; which at first ends in a closed extremity, but afterwards exhibits a wide orifice. It runs along the outer side of the Wolffian body, while its infundibulum, which is soon distinguishable, extends beyond and is entirely separate from that body.

The oviducts appear from the first in the form of white cylinders on both sides. They do not grow from below upwards, but are formed in their entire length from the commencement; nor are they constructed out of a membranous lamina, rolled together, as Meckel supposed; but are in the beginning solid, and become gradually hollowed out into a tube. In this way also is formed the infundibular opening of the tube into the abdominal cavity.

Two oviducts exist originally in all birds, but as in this class the right ovary shrinks and disappears, so the right oviduct becomes lost, by gradually contracting and shortening from above downwards. †

In mammals, before the distinction of sex becomes apparent internally, there is seen, running along the Wolffian body of each side in every embryo, a duct, which, according to Müller, may represent either a vas deferens, or an oviduct. These ducts lie upon opposite sides of the germ glands, which may become afterwards testis or ovary.

Soon afterwards the internal organs begin to exhibit a distinction of sex. This is indicated in the future male by the duct, which runs along the outer side of the Wolffian body, sending off a white granular projection, extending towards the testis, which is met by a similar projection, given off by the upper end of the testis, and these two by their union form the rudiments of the epididymis. So that in the male mammal a new connexion is established between the duct, which afterwards becomes vas deferens, and the testis, without any agency from the Wolffian body, but through the development of new material.

In the female these projections are wanting, both from the excretory duct and from the ovary. The latter remains attached only to the Wolffian body by a simple fold. The upper end of the duct, which runs over the Wolffian body, projects somewhat beyond that body inferiorly, and terminates here in a globular swelling, in which an aperture is formed at a later period.

As the Wolffian body becomes atrophied the portion of the duct which takes its course over it, and which was previously straight, begins to be tortuous in the male, while in the female it remains straight, but becomes wider. Out of corresponding portions of the duct are formed, in the male, the head of the epididymis, and in the female the infundibular end of the tube, while the inferior free portion of the duct, after it has quitted the Wolffian body becomes converted, in the male, into the vas deferens, becoming at the same time more and more elongated; but in the female the corresponding portion of the duct is transformed into the inferior division of the tube, or into the cornu of the uterus.*

In this stage of its development the incipient Fallopian tube is only beginning to be recognisable. It circumscribes the diminishing Wolffian body on its outer side in the form of a bow. Above the superior opening extends beyond that body, while below the short free portion becomes conjoined with that of the opposite side to form a single tube. These ducts have throughout the same breadth up to their union with each other.

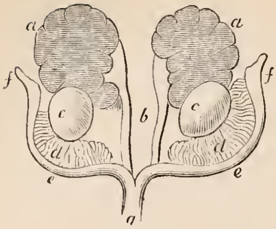
A division of the duct into uterus or cornu, and narrower Fallopian tube, is still nowhere perceptible, and the place of this latter division is only as yet indicated by the addition of the substance which afterwards becomes ligamentum rotundum. Between the oviduct and the ovary lies the atrophied Wolffian body of a dirty yellow colour, in part surrounding the ovary; but notwithstanding this contiguity the tubuli of the Wolffian body form no union between the Fallopian tube and the ovary. The duct, or future Fallopian tube, which had previously preserved a perpendicular direction, now takes, with the rest of these parts, a more sunken position. But it still lies close to the Wolffian body, from which it is separated by a narrow fold of peritoneum.

* See Müller's Bildungsgeschichte der genitalien. Düsseldorf, 1830.

† Prof. Quekett has pointed out to me, in the collection of the Royal College of Surgeons, a remarkable preparation by Mr. Tegetmeir, in which the right oviduct is developed in the common fowl.

* The researches of Kobelt upon this subject have been already explained under the head of development of the Parovarium.

Fig. 416.

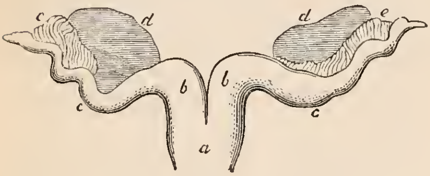


Genito-urinary organs of a fœtal sheep. (*After J. Müller.*)

a, kidneys; *b*, ureters; *c*, ovaries; *d*, Wolffian bodies; *e*, uterine cornua and Fallopian tubes; *f*, infundibular end of the tubes; *g*, middle portion of the uterus.

In older female embryos the Fallopian tubes, now more completely formed, are thicker and exhibit a somewhat undulating outline. The

Fig. 417.



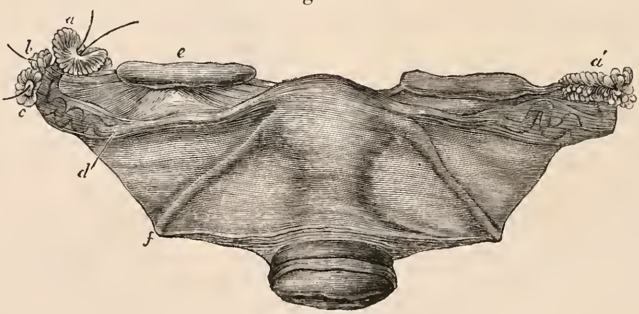
Internal generative organs of a fœtal deer. (*After J. Müller.*)

a, middle portion of the uterus; *b*, cornua; *c*, Fallopian tubes or oviduct; *d*, ovaries; *e*, remains of the Wolffian bodies.

Wolffian bodies, much reduced in size, may be found lying in a duplicature of peritoneum, between the ovaries and the oviducts. The inferior portion of the latter becomes widened, and the division between the tubes and the horns, or *cornua*, of the uterus is established; although the tube still remains relatively very broad, even up to its abdominal end.

In the human subject the opportunities for observation upon very early embryos being of not very frequent occurrence, the foregoing changes have not been so accurately traced in the first stages as in the embryos of birds and mammals; but all the examinations which have yet been made lead to the conclusion that the Fallopian tube has its origin in a duct similar to that already described. This, with the rest of the internal organs, is sufficiently developed by the third month of utero-gestation to leave no longer any doubt as to the sex. By this period the oviducts have nearly acquired that horizontal position which, from the fourth month onwards, becomes a more marked characteristic. In embryos of the fourth month the tubes run parallel with the now horizontally placed ovaries, whose elongated form corresponds with the tube in the greater portion of its length. By the end of this month the abdominal end of the tube is seen to be wide open, and traces of the fimbriæ are discoverable in its already fringed margin. The lower ends of the tubes are still not so completely united but that an indentation is perceptible at their point of junction, giving evidence of the still bi-corned condition of the uterus. From this period onwards the proper structure of the tube wall appears to grow with greater rapidity than the fold of peritoneum by which it is invested; so that in advanced embryos, and in the fœtus at term, the oviduct is usually found of a tortuous or serpentine form, its windings being easily distinguishable through the peritoneal sheath. The tube now much exceeds the ovary in length, and its infundibulur end is beautifully margined with delicate fimbriæ (*fig.* 418.).

Fig. 418.



Uterus and appendages of human fœtus at term. (*After Richard.*)

á, pavilion of the left side; *a*, the same of the right side (below it, in this specimen, is the remarkable variety of two separate accessory pavilions *b* and *c*); *d*, Fallopian tube, exhibiting numerous sinuosities in its outer half; *f*, round ligament; *e*, ovary.

Abnormal Anatomy of the Fallopian Tube.

Defect and Imperfect Development. — Absence of the Fallopian tube is of infrequent occurrence, and is usually observed in cases where there is a coincident deficiency of the uterus or ovary.* But when the two latter

* Meckel, Handbuch der Patholog. Anatomie, B. I.

organs are perfectly formed it is exceedingly rare to find a deficiency of the oviduct.

The oviduct may be deficient either upon one or both sides. Heusinger * has recorded an example of deficiency of the ovary and Fallopian tube of one side.

Chaussier † met with a remarkable example of a woman who, notwithstanding the absence of one ovary and tube, and even of one side of the uterus, bore ten living children; and whose death shortly after her last confinement afforded him the opportunity of ascertaining this peculiar condition of the parts.

After the observations which have been made regarding the function of the Fallopian tube, it is hardly necessary to observe here that deficiency of both tubes will be necessarily productive of permanent sterility; although absence of the tube of one side, as in the case of Chaussier, just quoted, need not entail any such consequence.

Unusual shortness of the tube and the absence of the fimbriæ have been also accounted as causes of sterility; but the former, if associated with a very short ligamentum ovarii, would have no such effect, and could be only accounted a relative deformity when the ovary is placed at an unusual distance from the uterus, so as to be beyond the grasp of the infundibulum; while the latter peculiarity, as already shown, may be merely the result of age.

Peculiarities of Construction. — Several Pavilions on the same Tube. — M. Richard, to whose researches regarding the Fallopian tube reference has been already made, has pointed out a previously unobserved condition of this part. In examining the appendages of the uterus in thirty women, he met with no less than five examples of this singular formation, which he thus describes:

"At a distance varying from several millimetres to 2 or 3 centimetres behind the normal pavilion, are observed upon the course of the tube one or more accessory pavilions, formed like that which terminates the oviduct, of a mucous membrane divided into fimbriæ. When the fringes of this pavilion are floated under water, they are observed to be pierced by an aperture leading into the canal of the tube; and a probe introduced into this orifice may be made to escape either by the ostium abdominale, or by the ostium uterinum, according to the direction in which it is passed. Thus, then, the canal of the tube can, in certain cases, open into the cavity of the peritoneum by several distinct orifices."

The first of M. Richard's cases occurred in an adult, and is represented in *fig.* 408.

"There is a normal pavilion of somewhat irregular form, and below it, at several millimetres distance, a small opening, surrounded by two small fringes, covered on their inner surface by mucous membrane; while the serous membrane terminates abruptly on their outer surface as in the true pavilion. A probe introduced escapes by one or other orifice indiscriminately."

The second example (*fig.* 418.) occurred in a fœtus at term. The tube of the left side terminates in a single pavilion, but that of the right, besides its terminal pavilion, exhibits also two little secondary pavilions, communicating each by a special orifice with the canal of the tube.

But the most interesting example is that shown in *fig.* 419. from a woman who aborted at the sixth month. The terminal pavilion, represented here of the natural size, exhibits a richness of fringes and folds rarely seen.

Fig. 419.

Extremity of Fallopian tube (human) having two pavilions. (After Richard.)

a a, fimbriæ of the terminal or normal pavilion, exhibiting an unusual richness of folds; *b b*, accessory pavilion in the side of the tube, having two distinct orifices separated by a valvular fold; *c c*, a bristle introduced at the terminal pavilion escapes by one of these lateral orifices, but cannot be made to pass out by the other, or to enter the uterus on account of the valve; *d d*, a second bristle introduced from the lower end of the tube escapes by the other orifice of the accessory pavilion, but cannot be made to penetrate as far as the terminal infundibulum.

* Heusinger's Zeitschrift für die organische Physick, II. 2.

† Busch. Das Geschlechtsleben des Weibes, B. IV. p. 348.

Below this large pavilion is another, the fringes of which are large and floating. This abnormal pavilion exhibits two orifices separated from each other by a valve, which, being prolonged into the canal of the tube, interrupts all communication between that part of the canal placed above and that below it. The valve is formed of a fold of mucous membrane. A probe introduced by the abdominal orifice of the tube escapes by one of the two orifices of the supernumerary pavilion, whilst one passed from the uterus appears at the other orifice of the same accessory pavilion.

M. Richard points out a very important influence which these abnormal openings may have upon the functions of the oviduct. An ovum having entered the terminal pavilion, if while endeavouring to gain the uterus it is directed along the wall of the canal which is opposite to the accidental opening, it will reach the uterine cavity; but if, instead of coursing along the wall opposite to the solution of continuity, it descends along this wall itself, then it will almost inevitably escape by this abnormal orifice, and will fall into the peritoneal cavity. Now, if this ovum has not been fertilised, nothing remarkable will ensue upon its escape into the peritoneum; but if the contrary, then it is possible that the fertilised ovum having escaped from the canal which should conduct it to the uterus will give rise to an abdominal pregnancy.

Displacement of the Fallopian Tube. — This is, perhaps, one of those conditions of parts which would be the least likely to be detected during life, and it may on that account have been often overlooked. It is of necessity associated with displacements of certain other organs, whenever such displacements occur; as, for example, with prolapsus inversion and retroversion of the uterus. In extreme prolapsus or procidentia uteri the tubes, along with the ovaries, are carried down and occupy a position on either side of the prolapsed organ, and between it and the walls of the inverted vagina, while in inversion the tubes are contained in the pouch formed by the reversed uterus.* In this latter case the relative situation of all the parts is so altered that the uterine orifices of the Fallopian tubes may be sometimes discovered as forming oblique openings in the upper part of the vagina.† But displacement of the Fallopian tube may occur alone, and constitute a true hernia. Such an occurrence is recorded by M. A. Bérard.‡ In this case the displacement took the form of a crural hernia, which was at first reducible, but after gradually increasing in size it could be no longer reduced. As fluid was distinguishable within the hernial sac a puncture was made, but peritonitis ensued, followed by death; and upon examination it was found that the sac contained nothing but the hypertrophied Fallopian tube.

* See *figs.* 470 and 471.

† Patholog. Museum, Roy. Coll. of Surg. Lond No. 2654.

‡ Revue Médicale, Mai 1839.

Meissner* has collected three other cases of hernia of the tube, one of which was congenital. These are all instances of inguinal hernia of the tube. In the "Journal für Geburtshelfer†" an instance of displacement of another kind is recorded. The left Fallopian tube had escaped through a rent in the walls of the vagina near the os uteri, and descended as far as the labia, so that the fimbriæ could be easily distinguished during life.

The most common displacements of the Fallopian tubes are those which result from adhesions consequent upon inflammation of their peritoneal coat. Such adhesions constituted by bands or extensive surfaces of false membrane, tie down the tubes to surrounding parts, and in most instances effectually prevent the performance of their proper functions; as where the tubes are adherent to the uterus, the sides of the pelvis, or the bladder or intestines. But the union is most commonly found to have taken place between the extremity of the tube and some part of the surface of the ovary, so that these are inseparably united together (*fig.* 409.), and very frequently in some abnormal position (*fig.* 420.)

Obliteration of the Fallopian Tube. — In advanced life a natural contraction of the tube takes place, and the fimbriæ also diminish and lose their luxuriance of form; but it frequently happens that, independently of these natural changes, and even at an early period of life, the tubes are found nearly or entirely obliterated. Such obliteration may be occasioned by tumefaction of the lining membrane of the tube, or by a collection of inspissated mucus in some part of the canal; or the entire calibre of the tube may be obliterated by cellular formation (atresia tubæ).

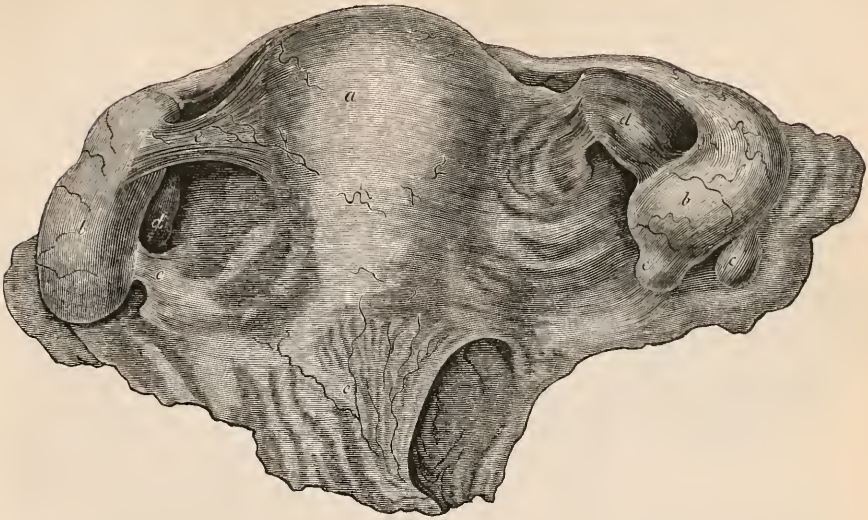
Occasionally calcareous concretions have been found obstructing the tube; and the same result has been produced by growths of a malignant kind.

The occlusion, however, is generally confined to the abdominal end of the tube. In these cases, usually, the fimbriæ are destroyed, the opening into the abdomen is completely closed, and the tube ends in a blunt cul-de-sac. Such a condition of parts is generally associated with an enlarged and tortuous state of the tube, the walls of which are usually thickened, and its canal filled with fluid. In such cases the obliterated end of the tube may remain free and unattached, but it is far more often found united inseparably to the ovary. This junction of the tube with the ovary by artificial adhesion is the most common of all the morbid conditions of the oviduct. It has been supposed by some to be the result of certain libidinous habits and practices; but this conjecture is not supported by any statistical evidence. The explanation given by Rokitansky, that this form of adhesion results usually from an extension of ca-

* Die Frauenzimmer Krankheiten, Leipzig, 1845, Bd. II. p. 203.

† Frankfurt u. Leipzig, 1787.

Fig. 420.



The Fallopian tubes tied down by false membranes to the ovaries and adjacent structures. (*After Hooper.*)
a, uterus; *b*, Fallopian tubes (the infundibula obliterated); *d*, ovaries; *e e*, bands of false membrane.

tarrhal inflammation along the lining membrane of the tube, which, spreading to the fimbriated extremity, gives rise to peritoneal inflammation in the vicinity of the orifice, so that the free terminations of the tube are bound down to the adjacent parts, seems to offer the truest explanation of the nature and origin of this peculiar condition of the parts. See *fig.* 409.

In some of these cases, however, there appears to have been something more than a mere process of exudative inflammation at work. The parts upon examination appear to have become blended by a combined process of absorption of the fimbriæ, and at the same time of firm agglutination of the infundibular base to the surface of the ovary; so that it may be difficult to find any precise line of demarcation between these parts, except that which a difference of colour may furnish.

Hyperæmia or congestion of the tissues of the tube is very commonly observed. It is apparently a normal state during healthy menstruation, but may be regarded as morbid when associated at other times with deep congestion of the uterus and ovaries.

A state of hyperæmia of the tube has been found associated with effusion of blood into its canal, and the escape of a portion of this fluid into the abdomen through the infundibular orifice.

Hyperæmia of the tube occurs as a seminormal condition in cases of tubal pregnancy.

Inflammatory lesions of the tube may present the characteristic conditions of acute or of chronic inflammation. The former is commonly seen in cases of puerperal metro-peritonitis, where the inflammation attacking usually the uterus first has extended to the ovaries and tubes. "The tubes are tumified and infiltrated; their mucous membrane is variously reddened, discoloured, excoriated, softened and everted at the fimbriated extremity. The passage of the tube is dilated, especially at its outer end, and filled with various products, purulent and sanious fluids, and in uterine croup with coagulable lymph, assuming the shape of a tubular concretion, the exudative process having extended from the uterus to the tube."*

But more commonly the traces of inflammation are found in the peritoneal coat, which highly congested and covered by flakes of lymph, partakes in the general inflammatory condition of the adjacent serous surfaces.

In the non-puerperal state, or as a sequel of puerperal affections, inflammation usually takes the form of catarrh or blennorrhœa of the mucous membrane of the tube. The usual evidences of such an affection are, a certain amount of tumefaction of the mucous lining, with thickening of the delicate plicæ covering it, and dark congestion of the capillary vessels. Within the tubal canal are found collections of mucus variously coloured, being sometimes viscid, or occasionally cream-like, yellow and purulent (*fig.* 421.).

The chronic inflammations of the serous coat of the tube, which result in various adhesions of this part to surrounding structures, have been already noticed.

Collections of fluid within the tube result from a combination of two or more of the foregoing conditions. These fluids consist of blood, menstrual fluid, mucus, serum, or pus, and sometimes of these in various states of admixture.

Collections of blood, or of a bloody fluid within the tube, are occasioned by hyperæmia of

* Rokitansky. Patholog. Anat. Vol. II. p. 326.

the tube-walls, whose over-distended capillaries relieve themselves by sanguineous effusion. In such a case, if both the orifices of the tube are patent, the fluid may escape into the uterus, or possibly, by the infundibulum, into the cavity of the abdomen. Of such

Fig. 421.

The Fallopian tubes thickened by inflammation, and distended by collection of fluid. (After Hooper.)
a, uterus; *b*, distended tubes; *c*, thickened lining of the same; *d*, round ligament.

effusions there are many examples on record. Or should the abdominal end of the tube be closed in the manner already described, and should the uterine end also be temporarily obstructed, as, for example, by slight congestion of the mucous lining at this point, then the blood, having no outlet, will continue to accumulate within the tube, and a distension of the parietes, more or less considerable, will result.

But all collections of blood within the tube are not necessarily the result of hæmorrhage. The menstrual fluid has been frequenly observed to have accumulated here. And these accumulations may occur under various circumstances. Thus, in the case of imperforate hymen, when the menstrual function has been established for some time, this fluid, after collecting behind the obstructed orifice of the vagina, gradually collects in and distends the walls of the uterus, and ultimately mounts up into the Fallopian tubes, distending them also in the same manner as the uterus.

But atresia of the vagina or uterus, causing such accumulations, is not necessarily congenital, but may be consecutive on adhesive inflammation attacking these parts; as in the instance of a woman, whose case is related in the American "Journal of Medical Sciences,"* and who, after her second confinement, had an attack of metritis, terminating in cohesion of the uterine walls and consequent occlusion of the cavity of the uterus. Behind this obstruction the menstrual fluid accumulated until the Fallopian tubes became so enormously distended that at length one of them burst, and death resulted from the escape of the blood into the abdominal cavity.

Or lastly, the menstrual fluid may collect in the tube after the manner of the blood in the case just described, where both the orifices of the tube are obstructed. Of such accumulations I have met with many examples; and it is interesting to observe that here, as under many like circumstances, the walls of the tube usually become hypertrophied in proportion to the degree of pressure caused by the accumulations of fluid which they are called upon to resist.

These collections of menstrual fluid within the tube, which I have found to be considerable in some instances, where I have ascertained beyond question that death had taken place during a menstrual period, are instructive, as showing, upon strong probable evidence, that the menstrual fluid is supplied in part by the walls of the Fallopian tube as well as by those of the uterus itself. For I have seen it in cases where both orifices of the tube were obstructed; and therefore in cases where it was not probable that the fluid could have regurgitated from the uterus into the tube.

Collections of serous fluid. Hydrops tubæ Hydrosalpinx.—In catarrhal inflammation of the mucous lining of the tube, whether oc-

* No. XXXV.

curring in the acute or chronic form, the fluid, secreted more abundantly than in a state of health, may find vent by either or both of the tubal orifices, so long as these remain pervious.

It is probable that in this affection the superabundant fluid flows generally by the lower orifice into the uterus, and so escapes per vaginam, constituting one of the numerous forms of "leucorrhœa." But if both extremities of the tube are closed, then, as in the case of hæmorrhage or menstruation occurring under like circumstances, the fluid collects within the tube and mechanically distends its walls.

The pressure producing this distension, when operating in only a slight degree, causes a nearly equable enlargement of the tube, so that its natural conical shape is still preserved. But as the quantity of fluid increases, the thinner and less resisting portions of the walls, which lie towards the distal extremity, give way more rapidly than those at the proximal end; and the tube, after becoming irregularly tortuous, is at length converted into a series of sacculi, the largest of which, usually of a pyriform shape, occupies the extremity of the tube (*fig.* 422. *d*).

From the irregularity with which different portions of the tube walls dilate under the pressure of the accumulated fluid, it often happens that several angles are formed by the sudden bending of the parietes, and at these points the tube walls, extending inwards, constitute so many valvular projections which partition the tube into several irregular chambers, communicating together by narrow orifices. Such a condition of parts may be frequently observed upon both sides of the body, as in *fig.* 422., where both tubes are affected in the same manner although in unequal degrees.

Fig. 422.

Distension of the Fallopian tubes, with obliteration of both orifices. (*After Hooper.*)
a, uterus; *b*, vagina; *c*, os uteri; *d* and *f*, Fallopian tubes; *e*, ovary.

When these dilatations have attained to any considerable size the condition of the lining membrane of the tube becomes altered, so that the mucous gradually acquires the character of a serous surface, and the fluids collected within these sacculi present the ordinary condition of the fluids of serous dropsies.

The more simple of these fluids are thin, serous, and nearly colourless, and may be more or less albuminous. Not infrequently, however, they contain flocculi, or are thickened by the admixture of various yellow, brown, or chocolate coloured denser fluids, consisting chiefly of pus and disintegrated blood.

The quantity of fluid does not commonly exceed a few drachms, and in ordinary experience six or eight ounces would be a rather large accumulation. Yet it is certain that sometimes a much more considerable collection has been observed.

Thus in "Bonnet's Sepulchretum Anatomicum *," a case is given in which one of the tubes held thirteen pounds of fluid; and De Haen † mentions an instance in which the hypertrophied tube weighed seven pounds, while the quantity of fluid contained in it amounted to thirty-two pints.

Other cases, of more or less authority, have been recorded, in which the collection of fluid has been estimated at 112, 140 and 150 lbs. But it is exceedingly doubtful if the tube walls are capable of dilating to the extent that would be necessary to support so large an amount of fluid without laceration. For it is very well known that in tubal pregnancy rupture of the tube almost always occurs before the middle period of gestation is reached; and even in those cases where the reports are founded upon post-mortem ex-

* Lib. III. Sect. XXI. Obs. 39.
† Rat. Med. Tom. III. p. 29.

amination it is very possible that a part of the fluid was contained in the ovary, for a concomitant enlargement of both tube and ovary is a very common occurrence, as in the case represented in *fig.* 422.; and on this account no record of any very considerable dropsy of the Fallopian tube should be considered as complete, unless the condition of the corresponding ovary is also mentioned.

Collections of puriform fluid in the tube. — *Abscess of the tube.* — The presence of pus in the Fallopian tube is most frequently associated with suppurative puerperal inflammation of the uterus and its appendages generally. But it may also occur independently of the puerperal state, and as a consequence of catarrhal inflammation of the mucous lining of the tube which may have passed into the suppurative stage. These cases differ from the foregoing, not only in the nature of the contents of the tube, consisting here of pus or of puriform fluids with admixture of other inflammatory products from the lining membrane of the tube; but also in respect of the great tendency which is here observable to the formation of adhesions and the establishment of fistulous openings into adjacent parts, as into the bladder, intestines, or peritoneum, into which cavities these fluids are occasionally discharged.

Cysts containing fluid attached to the tube.— Very commonly there may be observed one or more cysts containing a small quantity of transparent fluid, attached by a narrow peduncle to the tube, and particularly to the distal extremity (*fig.* 368. *e*). The nature of these cysts has been already explained. (See p. 597.) They can only be regarded as morbid when they attain to an unusual size, as in *fig.* 421. They are occasionally found as large as a nut, but they very seldom exceed, and indeed do not often attain even to this size.

Fibrous tumours. — One of the most remarkable points of difference between the morbid conditions of the Fallopian tube and of the uterus respectively is the very great rarity of the occurrence in the former of those fibroid growths, which in the latter constitute its most common abnormal peculiarity. Nothing can mark more distinctly the difference of texture between these two parts than this very characteristic circumstance: since it is now known that the peculiar fibrous tumour of the uterus is formed at the expense of the natural tissues of that part. Occasionally, indeed, small fibrous tumours are found in the parenchyma of the tube, but these never attain to any considerable size. These occasionally undergo calcification, from a deposit of earthy material in their texture, and thus form little masses of stony hardness which project from the walls of the tube, and are covered by its peritoneal coat.

Tubercle is occasionally formed in the Fallopian tube. It occurs there usually in the form of tuberculous infiltration, which, in the opinion of Rokitansky, affects chiefly the mucous membrane of the tube. The occurrence of tubercle here presents nothing remarkable enough to call for further special description.

Cancer of the tube is not a common occurrence. I have never met with it independently of cancer of the ovaries or uterus; but when either of the latter organs are extensively affected, the tubes are also occasionally involved. Upon the malignant diseases of the Fallopian tube most pathological writers are nearly silent; nor has our literature been enriched by any considerable number of special records bearing upon this point in Pathology.

Rupture of the Fallopian tube.— Spontaneous laceration of the walls of the tube occurs sometimes as a result of over-distension, or too great attenuation of its tissues, whereby the parietes are rendered no longer capable of resisting the increasing pressure of the fluids accumulated within. In this way large collections of serous, purulent, or sanguineous fluids are sometimes poured out into the cavity of the abdomen, unless, indeed, by the previous adhesion of the walls of the tube to surrounding parts, the point of rupture is directed to some neighbouring hollow viscus by which the fluids escape externally. But rupture of the tubes will most frequently happen in connexion with the tubal form of extra-uterine gestation, which is next to be described.

Detention and abnormal Development of the Ovum in the Oviduct. Tubal Gestation. Graviditas tubaria. — This constitutes a second species of those aberrant forms of gestation, commonly termed extra-uterine, one of which has been considered under the title of Ovarian Gestation, (p. 586.)

It has been already shown, that one principal office of the Fallopian tube is the conveyance of the ovum from the ovary, or place of its first formation, to the uterus, or seat of its final development; and that the ovum, whilst in transitu, not only becomes impregnated, but also exhibits certain indisputable evidences of commencing development, which, however, has usually advanced only a few stages by the time that the ovum enters the uterine cavity. The tube, therefore, as well as being an oviduct, is also the seat of normal impregnation; whilst, in addition, it serves to protect and possibly, in some slight degree, to add to the material of the ovum, although the actual operation of the tube walls upon the surface of the ovum in this respect must necessarily be very slight in the mammalia, since it so rarely happens that any increase in its size is perceptible from the time of its quitting the ovary to that of its reaching the uterus.

But the impregnated ovum, instead of entering the uterine cavity, may be accidentally detained in the tube, and undergo further development there. The extent to which this development may proceed will depend in a great measure upon the capability of expansion of the tube walls; a circumstance which seems to vary greatly in different individuals, and also in some degree according to the portion of tube which the ovum occupies.

The differences observable in this latter respect have led to a division of cases of tubal gestation into three varieties, viz. tubo-ovarian, tubal, and interstitial.

In the first variety, *graviditas tubo-ovaria*, the ovum becomes developed in a sac, of which a principal portion appears to be furnished by the hypertrophied walls of the infundibular end of the tube, and the proper tissue of the ovary combined. In the second, *graviditas tubaria*, the developed ovum occupies some part of the canal of the free portion of the oviduct; while in the third, *graviditas interstitialis*, the seat of development of the ovum is that part of the tube which traverses the uterine walls.

In the first, or *tubo-ovarian* variety, the parts supplying the principal foundation of the cyst, which surrounds the fœtus, are in the first instance probably chiefly normal structures; and it is easy to understand how, during the progress of growth of the ovum, when the limit of expansibility of these parts has been reached, there may be superadded to them materials for the extension and further growth of the cyst walls; and in this way are apparently formed these large sacs, or artificial uteri, which have been sometimes observed to surround a fully developed fœtus, and which in the course of their growth have come to include omentum, mesentery, or intestine, and other portions of the abdominal viscera or parietes, by which the sides of the sac become strengthened and enlarged.

As in the case of ovarian gestation formerly described, so in the varieties termed ovario-tubal, it is only when death has taken place during the early stages of formation of these embryo-bearing cysts that the exact nature and relation of the parts originally composing them can be made out. Hence the difficulty of determining, in more advanced stages of gestation, when other parts have been superadded, in what precise situation the development of the ovum was commenced. And hence the probability that some at least of those cases which have been recorded from time to time as examples of the fœtus developed in the cavity of the abdomen, and among the intestines (*graviditas abdominalis*), may have been originally cases of the tubo-ovarian variety, in which the cyst walls, commencing their formation by the artificial union of the expanded termination of the oviduct with a portion of the ovarian parietes, have in the course of their growth come to include many other parts.

The second variety, which includes all cases strictly termed tubal (*graviditas tubaria*), constitutes by far the most common of all the forms of extra-uterine gestation. Here the ovum is developed within some part of the free portion of the tube, whose walls appear, from the examples which most of our museums furnish, to be capable of a very limited degree of expansion in most individuals. Hence, when the ovum has attained to a certain size, and usually by the time that the second or third month of gestation has been reached, rupture of the tubal wall occurs, followed by rapid death from hæmorrhage. And thus the parts are usually obtained for examination in such a state as to leave no room for question regarding the precise seat which the ovum occupies, and the nature of the parts enclosing it. For in these cases of early rupture the tube has contracted no adhesions with surrounding parts, and the walls of the embryo-bearing sac are formed of the parietes of the oviduct alone.

The third variety of tubal gestation, distinguished by M. Breschet under the title of *Graviditas in uteri substantia;* and by Professor Mayer, of Bonn, as *Graviditas interstitialis*, has been made known, particularly by an essay of the former devoted to this subject.*

This variety differs from the last mentioned chiefly in the circumstance, that the seat of development of the ovum is that portion of the canal of the tube which passes through the solid walls of the uterus. Here the sac surrounding the fœtus is formed in a great measure at the expense of the proper uterine tissues, and consequently the parietes of these cysts exhibit under the microscope a very different composition from that which the tube walls show in the second variety.

In interstitial cases the walls of the sac surrounding the ovum sometimes attain in parts a thickness nearly equal to that of the gravid uterus. On section of these portions the appearance which they present is precisely similar to that of the gravid uterus itself. There is here seen precisely the same arrangement of large vascular openings, being the divided canals or sinuses which everywhere permeate the solid walls, in whose composition may be traced the same abundance of smooth muscular fibre, as in the ordinary gravid uterus.

Within such a sac, formed out of the walls of the tube in the first instance, and in the case of this third variety further strengthened by the addition of a large quantity of tissue derived from the uterus, the ovum lies, presenting its ordinary character of an external chorion and inner amnion; the fœtus or embryo itself, according to the period of gestation, being perfectly formed. The walls of the sac, being in this case usually much stronger than when the ovum lies nearer to the distal end of the tube, resist pressure for a longer time, and consequently the fœtus may attain a greater growth.

One of the most interesting questions connected with this subject is, whether a decidua is here formed. Schrœder van der Kolk, in his recent most valuable work on the structure of the Placenta †, answers the inquiry in the affirmative, in contradiction to the statement of Virchow ‡, by whom it is asserted that in the case of tubal gestation no decidua

* Mémoire sur une nouvelle espèce de grossesse extra-utérine. Par M. Breschet.

† Waarnemingen over het Maaksel van de Menschelijke Placenta. Amsterdam, 1851, p. 88. *et seq.*

‡ Virchow, ueber die Puerperal Krankheiten Verhand. der Ges. für Geburtshelfe. Berlin, 1848, B. III. s. 180.

is to be found in the tube. According to Schrœder, a decidua is here formed in tubal pregnancy, notwithstanding that in the walls of the tube glandulæ utriculares are entirely wanting. The villi are here embedded in little hollows of the decidua, upon whose walls the blood vessels terminate in open mouths, and thus the blood is poured out into the placenta. The decidua is, indeed, in this case firmer, and does not exhibit so many valvular openings as are present in an ordinary placenta; probably from the absence of the utricular glands. In this case, also, an epithelial layer derived from the decidua covers the villi, and serves at the same time as a means of junction between the parts.*

Associated usually with the abnormal development of the ovum in the oviduct is the formation of a decidua in the uterus, the nature of which structure will be considered in a subsequent portion of this article (pp. 635. 652).

And here it naturally occurs to inquire into the probable causes of the development of the ovum in a situation so unfavourable to its further and complete evolution. Since, notwithstanding the wonderful power of adaptation which is in these cases exhibited by the parts immediately surrounding and containing the ovum, it is plain that the oviduct however altered, yet, on account of its peculiar form and texture, can but inadequately supply the offices of a uterus. It can serve but imperfectly for the nutrition and protection of the fœtus, and not at all for its expulsion, even should the latter reach the term of its dependent or intra-uterine life.

One of the most remarkable circumstances relating to this curious subject, is the fact first noticed, I believe, by Dr. Oldham, that in a large number of cases of tubal gestation, the corpus luteum, corresponding with the ovum impregnated, is found in the ovary of the opposite side to that of the tube in which the ovum is developed. Thus if the left Fallopian tube contains the ovum, the right ovary will often display the corpus luteum of a corresponding date, and *vice versâ*. Not being at first aware of Dr. Oldham's observation, I had myself noticed the same circumstance in repeated instances, and had arrived at the same conclusion as he has done in explanation of it, namely, that at the time of the ovum quitting the ovary, the tube of the one side embraced the opposite ovary, and conducted away the ovum, which being impregnated in the ordinary way, and then being delayed at the angle formed by the bending of the tube, has its further progress obstructed at that point until it attains too great a size to admit of its subsequently passing the lower orifice and entering the cavity of the uterus.

If it be objected that this explanation is not satisfactory, because it assumes the apparent improbability of the fimbriated extremity of one Fallopian tube being able to grasp the opposite ovary, then I can point to a preparation in the Cambridge University Anatomical Museum *, in which both the Fallopian tubes grasp the same ovary to which their extremities are affixed by morbid adhesion.

Another and very different explanation of this remarkable circumstance of the impregnated ovum and corresponding corpus luteum being found on opposite sides, has been given by Dr. Tyler Smith †, who believes that the ovum, after descending the Fallopian tube of one side, traverses the upper part of the uterine cavity, and ascends the opposite oviduct, where it becomes developed. I might also furnish the advocates of this doctrine with an argument founded upon a most interesting and curious observation of Bischoff, which appears to have been overlooked, but which would at first sight seem to support this view. Bischoff, in his essay on the development of the ovum in the dog and rabbit, frequently noticed a remarkable apportioning of the ova between the two cornua of the uterus, so as to equalise their number on the two sides, when these had been originally unequal, as shown by the number of corpora lutea found in the ovaries. Thus, in the case of a bitch whose right ovary exhibited one, and the left ovary five corpora lutea, each half of the uterus contained three ova, so that two of the ova must have travelled across from the right to the left side. But it must be observed, that in the cases recorded by Bischoff the ova never ascended the Fallopian tube, but only travelled from one cornu of the uterus to the other.

When, therefore, we take into consideration the great difference between the solid uterus of man and the intestine-like organ of the mammalia, on which these observations were made, there appears to be great difficulty in supposing that the ovum could after once arriving at the uterus again enter an oviduct, especially when also it is remembered that while the conical form of the Fallopian tube, whose smallest aperture is towards the uterus, constitutes a provision for ensuring the arrival of the ovum there, this arrangement would greatly diminish the possibility of a retrograde movement taking place in the human subject, if indeed it would not altogether prevent it.

But to those cases of tubal gestation in which the corpus luteum is found in the corresponding ovary, neither of these explanations would apply. Here it is only necessary to suppose, that either the developmental changes already described as occurring normally to the ovum in the tube, have proceeded more rapidly than usual, or else, that the ovum, having been accidentally delayed for a longer time than ordinary in transitu, had acquired too great a magnitude to admit of its passage by the uterine orifice, even admitting, as some have supposed, that this orifice may, to a certain

* Upon this point I do not here give any observations of my own, as I am preparing these for publication in another form.

* No. 722.

† Lancet, No. xv. vol. i. 1856.

extent, dilate, for the purpose of allowing the ovum to pass, just as the os uteri dilates at the time of labour.

UTERUS.

Normal Anatomy.

(Syn. *Womb*, *Mother*, Eng.; Μήτρα, Ὑστέρα, Δελφύς, Gr.; *Uterus*, *Matrix*, Lat.; *Utero*, Ital.; *Matrice*, Fr.; *Bärmutter*, *Gebärmutter*, *Fruehthälter*, Germ.; *Baarmoeder*, *Lijfmoeder*, Dutch.)

The uterus is that segment of the generative track which lies between the lower extremities of the Fallopian tabes and the fornix or upper end of the vagina. In man it is normally formed by the complete coalescence of the two uterine cornua, which in most of the mammalia remain more or less distinct constituting the bicorned or divided uterus. These, in man and the quadrumana, unite to form a single symmetrical organ, serving for the passage of the seminal fluid, and for the reception, protection, nutrition, and final expulsion of the mature ovum.

The uterus is not altogether peculiar to the female. Like the mammary gland, it has its representative in the male, though only in a rudimental state. The existence of such a rudimentary organ is more easily shown in the male of many mammalian animals than in man, in whom, perhaps, it is the least conspicuous, and where its presence, as a type of structure, can only be proved by a close study of homologies, and by the aid of those occasional exemplifications of the true relations of this part which the comparatively rare occurrence of hermaphrodite forms affords.

Situation and position.— The unimpregnated uterus is situated entirely within the pelvis, where it lies deep among the other pelvic contents, with many of which it is in immediate relation; the bladder lying anteriorly, the rectum posteriorly, the ovaries and Fallopian tubes laterally, the small intestines superiorly, and the vagina and perineum inferiorly with regard to it. These several parts, aided by the broad and round ligaments, serve to support the uterus and maintain it in its natural position. But this position will of necessity vary according to the condition of the neighbouring organs, and in some degree also with the varying postures of the body.

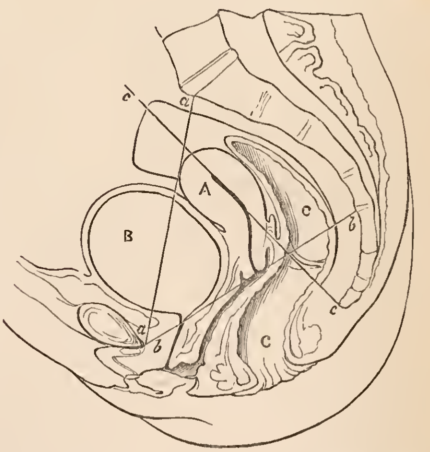
The nature and degree of the variations in regard to situation and position of which the uterus is susceptible will be more easily understood after the ligaments and other connections by which these movements are restrained have been described. At present it will be only necessary to observe that the motions of the uterus are restricted chiefly to three directions. First, the broad ligaments, which maintain the organ nearly in the median line, permit by their laxity a slight deviation towards either side. Secondly, a certain amount of ascent and descent is allowed by the structures which attach the uterus to the lower part of the pelvis. But the former of these movements will be limited by the utero-sacral ligaments, and the weight or pressure of the superincumbent viscera; and the latter also especially by the same ligaments, and to a certain extent by the support derived from the posterior wall of the vagina and the parts which close the pelvis below. Thirdly, the uterus enjoys a certain range of motion in the direction of a line drawn from pubes to sacrum in order to accommodate it to the state of fulness or emptiness of the adjacent viscera. For when the bladder is full and the rectum empty, the uterus will be carried nearer to the sacrum; and conversely, with an empty bladder and a distended rectum, the position of the uterus will be proportionately nearer to the pubes; and these alterations of position will be constantly and daily repeated.

But an equal degree of mobility does not belong to every part of the uterus; for while the movement of the cervix is limited by the attachment of the vagina and utero-sacral ligaments, the fundus is left entirely free to follow the alternate fillings and emptyings of the bladder. Thus a movement of nutation will result, the fundus uteri approaching the pubes and sacrum alternately; and this is probably the greatest range of motion of which any portion of the uterus is normally susceptible.

But allowing for these variations, there will still be an average position which the uterus occupies in the pelvis, and this may be assumed to occur at the time when the bladder and rectum are both moderately distended.

Under these circumstances, the position of the uterus relatively to surrounding parts will be in accordance with the accompanying sectional diagram (*fig.* 423.), representing the pelvic contents. Here A represents the uterus, B the bladder, and C the rectum, both of the latter being moderately distended.

Fig. 423.



Sectional diagram to show the normal position of the uterus in the pelvis.

At such a time the uterus, supported between the folds of the broad ligament, which constitutes a moveable dissepiment, dividing the pelvis transversely into two unequal parts, and sustained by the parts attached to it around and below, lies with its fundus directed obliquely upwards and forwards, while the cervix or neck looks downwards, and very slightly backwards towards the orifice of the rectum. The relative heights of these several parts are determined by two lines: the one, *a—a*, drawn from the lower border of the symphysis pubis to the promontory of the sacrum; the other, *b—b*, from the same point to the lower margin of the fourth sacral vertebra. Upon the latter the cervix will rest at a point near the centre of the line. The direction of the uterine body will be more conveniently shown by a third line, *c—c*, drawn through its axis. This line, if produced, will pass out of the pelvis upwards at a distance of $\frac{3}{4}''$ in front of the sacral promontory; and downwards, after traversing the posterior wall of the cervix, it will pass out about the centre of that wall, and impinge upon the extremity of the coccyx. The lower portion or cervix of the uterus being curved upon the body in the manner hereafter described, the direction of its canal will be downwards, and will be represented by a line drawn nearly perpendicular to the horizon.

Form. — The uterus belongs to the class of hollow muscles, with which it is associated on account of its cavity and the muscular character of its proper parietes. In many of the mammalia, the elongated form and general arrangement of the tissues gives to the uterus a resemblance to an intestine; while in man and the quadrumana, in whom it possesses a considerable degree of firmness and solidity, the shape more nearly resembles that of the urinary bladder.

The uterus has been compared to various objects, such as a flask, a little gourd or calabash, a pear, or a truncated cone. There is enough of similarity to these several objects, to excuse the comparison, yet the resemblance is not sufficiently close to render any of them an exact representative of that body; but perhaps the flattened pear conveys the best idea of the uterine figure, although the pyriform outline is somewhat broken by the attachment to its lateral borders of the parts usually termed appendages (*fig.* 368.). These should be, therefore, removed in order to display the proper boundaries of the organ (*fig.* 424. and 431.).

Dimensions. — The uterus does not attain to its full development until after the establishment of puberty. Previous to this period it remains but little altered from its infantine condition; but as the period of puberty approaches, and about the time when the mammæ, which have also until then retained their infantine state, begin to enlarge, the uterus rapidly increases in bulk and weight. It then soon reaches the size which, if unemployed, it maintains through the rest of life, only wasting, and becoming somewhat altered in figure by absorption of its tissues, as age advances; or, if employed in the process of reproduction, then undergoing a degree of temporary enlargement unparalleled by any other growth of structure in man, and subsequently returning, in part, though never entirely, to its former state.

The following are the average dimensions of the virgin or nulliparous uterus. The entire length from the centre of the fundus (*fig.* 424 *a*), to that of the anterior lip *b*, which gives the longest diameter, is $2''$, $3'''$—$7'''$.

Of this one half usually belongs to the body, and the remainder to the neck or cervix; but the proportional length of either of these parts may exceed the other by $1'''$—$2'''$.

The greatest breadth of the organ is found opposite to the point of attachment of the Fallopian tubes. Here the transverse diameter is $1''$, $3'''$—; at the point of junction of the cervix with the body $10'''$; about the centre of the cervix $12'''$; at the extremity of the cervix, opposite to the point of junction with the vaginal walls, $11'''$—$12'''$.

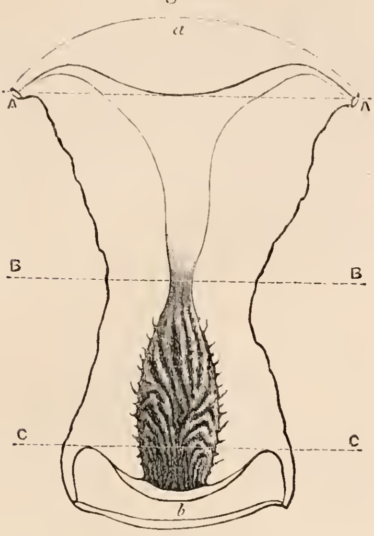
The antero-posterior diameter of the uterus is greatest about the centre of the body, where it measures in the nulliparous organ $11'''$—$12'''$.

Weight. — The weight of the adult virgin uterus, deprived of the appendages, is 9—12 drachms.

Regional divisions. — The uterus is divided primarily into a body and neck or cervix. Each of these is again subdivided, the upper portion of the body being termed the fundus, while the lower or terminal part of the neck is distinguished as its vaginal portion. These divisions, though to a certain extent artificial, are necessary, not only to facilitate description, but also to distinguish parts which exhibit great and important differences both of structure and function. So great, indeed, is the amount of structural and functional difference between the body and neck of the womb, as almost to justify these being regarded as two distinct organs.

The *fundus* is that portion of the body of the uterus which lies above an imaginary line, (*fig.* 424. A A,) drawn transversely across the organ from the point of attachment of one Fallopian tube to that of the opposite side. This portion of the uterus is of a very dense and firm texture. It is very slightly convex in the virgin state, but becomes considerably arched and expanded during pregnancy, when it forms, as it were, a vaulted roof to the organ. After parturition the fundus does not regain its former figure, but retains more or less of the rounded form which constitutes one of the points of difference between the nulliparous and multiparous organ. The fundus is that part of the uterus which, from its concealed position within the pelvis in the unimpregnated healthy state, is the least capable of being examined during life. It is of all parts of the uterus that which is the least subject to destructive disorganisation by malignant growths, frequently remaining unaltered in texture after the whole of the cervix has been destroyed by carcinomatous ulceration. On the other hand it is the part

Fig. 424.



Section showing the regional divisions of the uterus. (*Outlined ad Nat.*)

from which polypi, that are not cervical in their origin, most frequently arise; and it is very commonly the seat of those large hypertrophic growths of the uterine tissue, which are usually termed fibrous tumours. The fundus is also the part to which the upper portion of the placenta is most frequently attached.

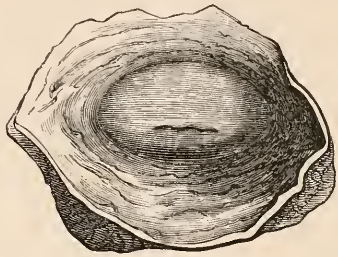
The body is included between the line above indicated, and another, B B, drawn through the narrowest part of the organ, or that point at which the tapering lateral walls of the uterus approximate in the greatest degree before they again diverge to pass into the cervix. The body of the uterus constitutes its principal portion. It is that part which, more than any other, expands to invest the ovum. It is freely supplied with blood-vessels, which, entering by the lateral border, ramify abundantly through the anterior and posterior walls. These walls are usually half an inch in thickness. They are separated from each other by a scarcely appreciable cavity, to be hereafter described, lying between the inner surfaces of the parietes. The extreme narrowness of this cavity is shown in *figs.* 427 — 430., which represent transverse sections of the uterine body, at various points between the fundus and internal os.

The cervix, or neck, (*fig.* 424. B—C), is a cylindriform prolongation of the uterine body, to which it serves as an excretory conduit. It is composed in part of tissues similar to those of the body, but the arrangement of these is materially different. The walls of the cervix measure $4'''$ in average thickness. Their inner surfaces are not in immediate contact like those of the uterine body; but diverge slightly to enclose a flattened spindle-shaped cavity, termed the canal or cavity of the cervix.

The situation of the widest or central part of this canal is indicated by an external lateral bulging of the walls of the uterine neck. The posterior part of the cervix receives a loose investment of peritoneum; but the whole or the greater portion of its anterior wall, as well as the lower or vaginal portion, is uninvested by that membrane.

The vaginal portion.—The lower extremity of the cervix (*fig.* 424. below, C C) projects

Fig. 425.



Os uteri, and vaginal portion of the cervix. Virgin. (*Ad Nat.*)

into the vagina in the form of a flattened cone. The length of this conical projection is about $4'''$. It is of unequal diameter. Transversely it measures $11'''$—$12'''$ at the base, and $6'''$—$7'''$ at the apex; but its antero-posterior diameters are only $7'''$—$8'''$ at the base, and $5'''$ at the apex; so that a section of this part will represent an ellipse. Around the base of this conical portion the walls of the upper end of the vagina are attached. The vaginal attachment constitutes the line of demarcation between the lower or vaginal and the upper or supra-vaginal division of the cervix. It should be observed that the end of the cervix does not lie, as is commonly supposed, exactly at the extremity of the vaginal canal, but that it projects into its upper wall, so that the upper vaginal wall is shorter than the lower by the whole antero-posterior diameter of the cervix (*fig.* 426. and 433.). This explains the difficulty which is sometimes experienced in bringing the cervix into view when a tubular speculum is employed, the sides of which are all of equal length. There can be no doubt that this peculiar position of the extremity of the cervix prevents the part from suffering injury in coitu, because the impulse of the intromittent organ is received upon the end of the vagina, and is distributed upon the adjacent parts, through the intervention especially of the utero-sacral ligaments. See further, p. 689.

At the apex of this conical mamelon is observed a transverse fissure $3'''$—$4'''$ in length. This is the lower or terminal orifice of the cervical canal, the os externum uteri, *fig.* 425., as distinguished from the os internum, *fig.* 431, *i*, which marks the commencement of that canal. The os externum is bordered in front and behind by two smooth lips, whose commissure on either side forms the lateral boundaries of the orifice. The lips constitute the terminations of the anterior and posterior cervical walls respectively. They are accordingly distinguished as the anterior and posterior lips of the os uteri. Their position and form are most conveniently shown in a vertical section of the part (*fig.* 426. and 433.). The anterior lip is the smaller; it projects but slightly into the vagina, but it lies at a lower level than the posterior one, on account both of the greater length of the anterior wall of the uterus, and also from the inclination of the upper part of the organ forwards. In an antero-posterior view, the anterior serves to conceal the posterior lip, which lies higher in the pelvis, both from the comparative shortness of the posterior uterine wall, and also from the tilting forward of the entire organ; nevertheless the posterior lip makes a greater projection into the vagina, because the walls of that canal are reflected off at a higher point upon the cervix posteriorly than anteriorly. This unequal form of the two lips doubtless gave origin to the term os tincæ, by which the older anatomists designated the part.

In no portion of the uterus is the difference between the nulliparous and multiparous organ so marked as in the vaginal portion of the cervix. After the birth of many children, this part becomes much enlarged, soft, flaccid, and of irregular form, with notched margins; but in the virgin it has uniformly the smooth, even, conical figure just described, while its consistence is nearly that of soft cartilage.

External surface.—The uterus, being a hollow or cavitary organ, possesses both an *external* and an *internal* surface. The external surface exhibits two faces, anterior and posterior; three borders, one superior and two lateral; and three angles, two superior and one inferior.

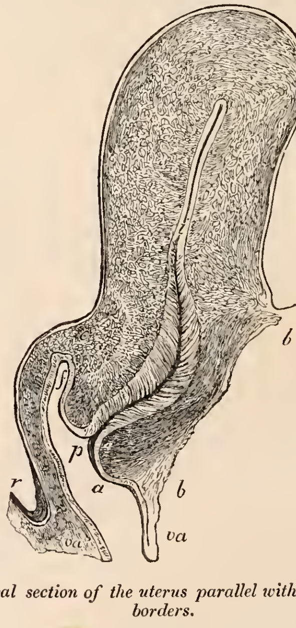
The anterior face is smooth, and gently convex in the transverse direction (*figs.* 427—430.), but often slightly curved from above downwards (*fig.* 426.). It is covered by peritoneum in all but its lower part, where this membrane is reflected off to give a covering to the bladder at a distance of not less than one fourth of the entire length of the uterus from its lower extremity. The posterior face is more decidedly convex; and in some subjects, especially in multiparæ, it exhibits a marked prominence along the median line, from which the walls proceed outwardly in two nearly level planes. These, meeting the less convex anterior walls at the lateral border, give to a transverse section of such an organ an outline more or less triangular (*fig.* 428.). The posterior face also receives an investment of peritoneum. The membrane here, after covering the entire posterior surface of the uterus, usually dips down to cap the upper extremity of the vagina. (*Fig.* 426. *c*—*r*.)

The superior uterine border is moderately convex; it extends from the point of entrance of one Fallopian tube to that of the other (*fig.* 431. *f f*). This border is entirely covered by peritoneum. The two lateral borders extend from the point of entrance of either Fallopian tube downwards to the lower extremity of the uterine neck, as far as the margins of the os uteri. These borders are flexuous, being convex above, concave towards and below the centre of the organ, again slightly convex about the middle of the cervix, and finally terminating at the os uteri, after having their continuity interrupted by the circular attachment of the vagina near the termination of the uterine neck. The lateral borders are uninvested by peritoneum; for it is here that the two laminæ of that membrane, which form the broad ligament, meet to inclose the uterus; and by these two lateral borders, the blood-vessels and nerves supplying the organ enter it without penetrating its outer or serous coat (*fig.* 428.).

The two superior angles are formed at the points of entrance of the Fallopian tubes. The inferior angle is occupied by the vaginal portion of the cervix and the os uteri.

Internal surface and cavities of the body and cervix. — It has been stated that the walls of the uterine body are in nearly close apposition internally, leaving only a small intermediate space, termed the cavity of the uterus, which is easily displayed by cutting through

Fig. 426.



Vertical section of the uterus parallel with its lateral borders.

a, anterior, and *p*, posterior, lip of cervix; *i*, internal os uteri; *v a*, vagina; *f*, fornix; *c*, loose connective tissue immediately above the fornix; *r*, point of posterior reflection of the peritoneum on to the rectum, forming the retro-uterine pouch or space of Douglas; *b b*, line of attachment of the cervix to the bladder. The peritoneum ceases at the upper *b*, in front. (*Ad Nat.*)

the substance of the organ. No just conception, however, of the real form or capacity of this interspace can be obtained by examining it with the aid of sections made in one direction only.

In order to obtain a correct notion of the form and extent of this cavity, it is desirable first to make a longitudinal section through the centre of the entire organ parallel with its lateral borders. The cavity or interspace is then indicated by a line running from below upwards, and terminating within half an inch of the fundus (*fig.* 426.).

The upper half of this line indicates the cavity of the *uterus;* the lower half, that of the *cervix.* The latter alone exhibits a true cavity; for here the parietes of the cervix are

Fig. 427.

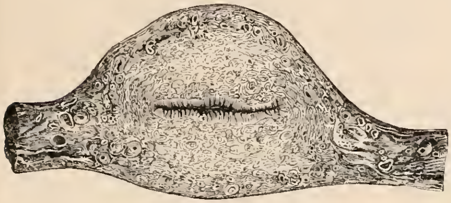


Fig. 428.

Fig. 429.

Fig. 430.

Series of horizontal sections of the uterus.

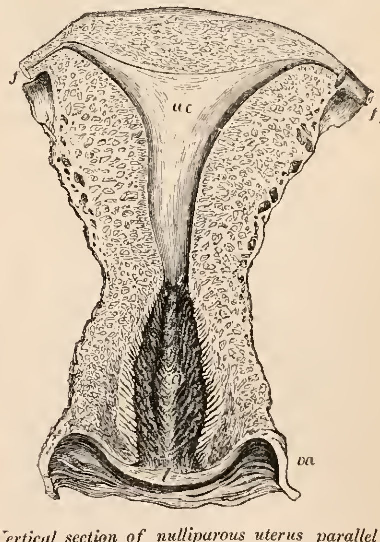
Fig. 427., just above the entrance of the Fallopian tubes. *Fig.* 428., in the centre of the cavity. *Fig.* 429., close to the internal os uteri. *Fig.* 430., the centre of the cervical canal. The upper or more convex border marks the posterior surface in each section. (*Ad Nat.*)

observed to diverge slightly, so as to leave a spindle-shaped canal traversing the whole length of the uterine neck (*fig.* 431. *c c*).

A second view is obtained by cutting completely through the uterus in the direction of its transverse diameter, and parallel with its extremities. If the entire organ be cut up into many such segments (*fig.* 427—430.), it is then seen, from the length of the central line, that the cavity varies in breadth, its widest part being in the segment which includes the extremities of the Fallopian tubes; whilst from this point downwards the line diminishes in length, until at the narrowest portion of the uterus, or that representing the commencement of the cervix, it measures only $1\frac{1}{2}'''$—$3'''$ in diameter.

But the most complete view of the interior of the uterus is obtained by a section carried through the centre of the organ, dividing it midway between its anterior and posterior walls. The entire cavity which is thus exhibited at one view is seen to be of a triangular form; its boundaries being formed superiorly by the fundus, and on either side by the two lateral borders, whilst in each angle is observed an aperture. The two superior openings are the lower orifices of the Fallopian tubes. The inferior opening leading to the cervical canal constitutes the os uteri internum (*fig.* 431. *i*).

Fig. 431.



Vertical section of nulliparous uterus parallel with its anterior and posterior walls.

u c, uterine cavity; *c c*, cervical cavity or canal; *i*, internal os uteri; *e*, external os uteri; *f, f*, Fallopian tubes; *v a*, vagina. (*Ad Nat.*)

Since the cavity in the interior of the uterine body has a triangular form, whilst externally the shape of the organ is more or less pyriform, it is evident that the parietes of this "hollow muscle" cannot have everywhere an equal thickness, for otherwise the form of the cavity would correspond with that of the external surface. But whilst the anterior and posterior walls exhibit an average and nearly uniform thickness of about 6‴, that of the lateral boundaries and of the fundus varies from 6‴ to 1‴. Hence the section of this cavity represented in *fig.* 426., which exhibits the organ as divided from before backwards, is described by a right line; whilst the section (*fig.* 431.) shows the cavity as bounded by three curves, the degree of curvature varying in different subjects, and being generally supposed to be always greatest and most marked in women who have never borne children.

This point has been much dwelt upon as serving to distinguish the nulliparous from the multiparous uterus. I have reason to think, however, that this observation has been again and again repeated without confirmation by an appeal to facts. For although the sides of the virgin uterus are often strongly incurved, yet in some uteri in my possession from young subjects who had not borne children, the walls of the cavity are nearly straight, and this is the form which they have in the fœtus (*fig.* 442.), and in undeveloped uteri (*fig.* 465.); whilst in other specimens, taken from women who had borne many children, the sides and fundus may be incurved in various degrees. Much will depend upon the mode in which the sections are made; for unless, in dividing the organ, the knife has passed exactly through the median line, a portion of either the anterior or posterior wall will be included in the section, and the apparent form of the cavity will be materially modified thereby.

Thus the uterine cavity in the unimpregnated state is nothing more than the narrow interspace between the flattened walls which are normally either in immediate contact, or are separated from each other by only a small quantity of mucus. The triangular form results from the confluence of three ducts or channels; viz., the two oviducts above, and the cervical canal below. The tubal canals, having passed through the substance of the uterus, expand trumpet-like into the uterine cavity, whilst in the same way the cervical canal traced upwards is prolonged, though more gradually, into the same cavity. But the perpendicular diameter of the uterus being always greater than the transverse, the form of the cavity, in so far as it is triangular, represents not an equilateral, but an isosceles triangle with incurved sides (*fig.* 431.).

By reference to these particulars regarding the form of the interspace between the uterine walls, we are enabled to explain many phenomena relating to the first entrance of the ovum into the uterus, and its mode of detention there, before it has become organically united to the uterine walls.

The cavity of the uterus is lined by a mucous membrane, the peculiarities of which will be afterwards more fully described. This membrane appears to the unaided eye nearly smooth, and is usually of a pale pink colour, except in those cases where death has occurred during menstruation, when it is of a deep red hue, and more or less plainly vascular. A moderate amplifying power, however, suffices to show that the mucous membrane is not smooth, but is perforated everywhere by minute apertures, which are the orifices of numerous ramified canals or follicles occupying the substance of the mucous membrane, and lying for the most part in a direction perpendicular to the surface upon which they terminate. A few folds are occasionally perceptible in the mucous membrane, these being seen chiefly in the neighbourhood of the tubal orifices.

The apertures by which the Fallopian tubes enter the upper angles of the uterus are so small as only to admit of the passage of a fine bristle (*fig.* 406.). That by which the cavity of the body communicates at its inferior angle with the canal of the cervix has an average diameter of 1½‴—3‴. This orifice is the os uteri internum (*fig.* 431. *i*).

The following are the dimensions of the uterine cavity:—length 11‴—12‴; breadth between the points of entrance of the Fallopian tubes 11‴—12‴; at the centre of the cavity 4‴; at the os internum 1½‴—3‴.

The cavity of the cervix consists of a flattened fusiform canal running through the centre of the uterine neck. The widest portion occurs about the middle, where the canal measures transversely 3½‴—6‴ (*fig.* 431. *c c*), whilst towards either extremity the parietes gradually approximate so as to leave a narrow aperture at each end; the superior aperture being the orifice already described as the os uteri internum, the dimensions of which have been given;—the inferior being the os externum, or os tincæ, which measures 3‴—4‴ in transverse diameter. The antero-posterior diameter of the canal at its widest part is not more than 1½‴—2‴. The entire length of the cervical cavity is 12‴—13‴.

The mucous membrane lining this cavity is probably not greatly inferior in extent to that of the uterine body. But on account of the smaller space in which it is contained, instead of forming an even layer, the membrane is here thrown into numerous folds or plicæ, having intermediate furrows, often traversed by lesser plicæ, which extend the secreting surface, and furnish a more considerable seat for those numerous mucous crypts which abound upon almost every portion of this structure.

The forms which the cervical folds or plicæ assume are sufficiently remarkable to have attracted the attention of anatomists at all periods. They are, however, so variable, that if twenty specimens be compared together, scarcely two will be found to present precisely the same arrangement. On this account it is difficult to furnish any description of them which shall be universally applicable.

Nevertheless, two forms appear to me to be more prevalent than others. In one a single prominent raphé occupies the centre of each wall of the cervix. (*Fig.* 431. *c c.*) Commencing sometimes at a distance of $1\frac{1}{2}'''$—$3'''$ above the margin of the uterine lip and extending upwards either centrally or to one side of the median line, and reaching as far as the internal os, it terminates here in a bulbous expansion, or branches out into numerous small ramifications. From either side of this median perpendicular fold are given off lateral plicæ, varying in number, but being usually not less than 6—9. These soon bifurcate once or twice, so that the number of folds will vary considerably, according as they are counted immediately at, or at some distance from, their line of junction in the central raphé. The uppermost pair of lateral plicæ, or those next to the raphé, often exhibit the same bulbous extremity; and these together fill the upper or narrowest portion of the cervical canal. Lower down, where the canal becomes wider, the lateral plicæ spread out on either side of the central raphé, the upper ones in an oblique, the middle and lower ones in a more horizontal direction. These soon bifurcate, and form a series of oblique, horizontal, or arched laminæ, whose arrangement varies much according to the fulness of the folds, the depth of the furrows between them, and the distance by which the laminæ are separated. If the latter are prominent and very closely set, their margins may overlie each other, like the branchial laminæ of a fish, so that no intermediate furrows are perceptible; or the folds, not being very prominent, may merely lie in apposition, leaving no visible interspace until they are drawn asunder; but when the plicæ are less full and prominent a furrow is perceptible between each. These furrows of necessity take the same direction as the plicæ by which they are bounded.

In another common form which the plicæ assume, the general lines of folds and intermediate furrows take a more vertical direction, so that sometimes as many as six or eight of the more central laminæ may be traced running down side by side to the very margin of the cervical lips (*fig.* 424.). Here often the two most central folds appear to run up from one end to the other of the cervical canal; but still commonly one of these is more fully developed than the rest; its upper bulbous extremity occupying the position in the narrow portion of the cervical canal, already described, while its lateral divisions being more numerous than those of the plicæ next adjoining, it takes the office of a raphé, though its position may be, as it often is, more or less eccentric.

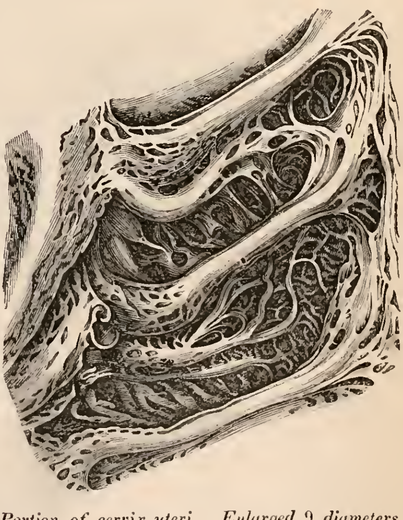
On either side of this principal fold the lateral plicæ arrange themselves, inclining more outwardly in proportion as they occupy a still lower place in the cervix. But in these cases the curves of the lateral plicæ are often very abrupt — the laminæ rising obliquely upwards, and then making a sudden downward bend like the ends of the leaves of a lily. This arrangement of the plicæ I think I have more often observed upon the posterior wall of the cervix, where the laminæ are usually thicker and bolder than upon the anterior wall, upon which the arrangement first described appears more commonly to prevail. But so various are the forms which the principal folds of the mucous lining of the cervix assume, that it is not possible to fix upon any one instance whose description, however minute and accurate, will serve as a strict example of the rest.

The more perpendicular the arrangement of the plicæ, the nearer is the approach to that form which is most commonly found in the terminal part, or neck of the uterus, in the mammalia generally, where the folds almost invariably take the direction of the long axis of the canal, reminding us of the arrangement of the plicæ in the Fallopian tube already described.

After repeated pregnancies these plicæ become much thickened and the folds more prominent, while their extremities exhibit a swollen and bulbous appearance resembling leaflets attached to the branch of a tree. Hence, apparently, the origin of the old term *arbor vitæ*, by which this structure was commonly designated; while to the more closely arranged plicæ, springing from a central shaft or raphé, the term *penniform rugæ* is more strictly applicable; and to those cases in which several parallel folds, after ascending obliquely, form a series of lateral arches, or suddenly bend over and then downwards, the title of *plicæ palmatæ*, or as some employ it, *palmæ plicatæ*, seems more appropriate.

Thus upon both walls of the uterine cervix the mucous membrane, being of greater extent than the surfaces which it lines, is gathered

Fig. 432.



*Portion of cervix uteri. Enlarged 9 diameters. (After Tyler Smith, and Hassall.)**

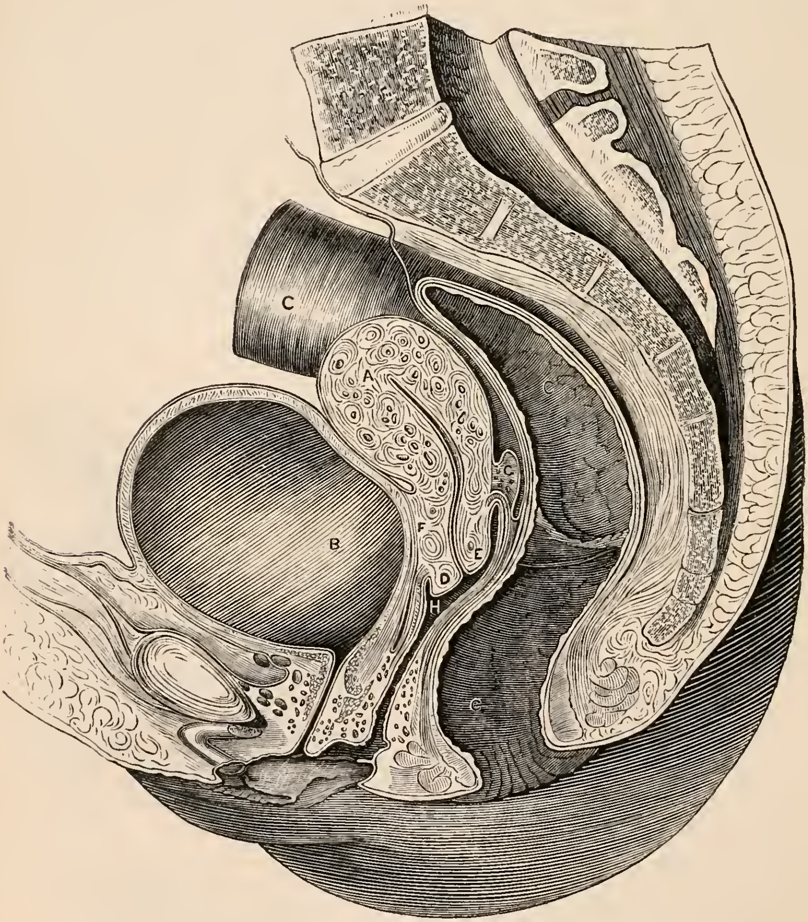
* This figure is from a valuable Memoir on the Pathology and Treatment of Leucorrhœa, in vol. xxxv. of the Medico-Chirurgical Transactions, 1852; where will be found also a description, with illustrations, of several of the natural and abnormal forms and conditions of the cervix.

into folds whose offices will be presently more specially considered. At the lateral lines of junction of the two cervical walls, where a crease or furrow is formed by the sudden bending of the parietes, an imperfect raphé is sometimes found, uniting a portion of the plicæ; but more commonly the laminæ of one surface either pass over and become united at their extremities with those of the opposite side, or else upon reaching the lateral angles they split up into smaller divisions, which are again gathered into the single folds upon the opposite side, their junction being then effected by the interposition of a cribriform surface.

The central raphé and lateral plicæ proceeding from it, under whatever form they may appear, constitute together a series of primary folds, from which others of a secondary order are produced. These emerge from either side of the lateral plicæ, and, crossing the furrows between them, subdivide again and again until the whole surface presents that cribriform aspect which can be just discerned by the naked eye, but cannot be accurately examined without the aid of the microscope. Here also are found in countless numbers these mucous crypts, which apparently furnish the peculiar secretions of this portion of the uterus (*fig.* 432.).

Structure and arrangement of the tissues composing the uterus.— The uterus is usually described as consisting of three coats, viz., an outer or serous, a middle or muscular, and an inner or lining membrane, commonly termed the mucous coat. But these coats cannot, like the three coats of an intestine, for example, be separately displayed, because each passes so imperceptibly into the others, that although to the naked eye an apparent distinction may

Fig. 433.



Section of female pelvis and its contained viscera. (*After Kohlrausch,*—reduced.*)

A, uterus; B, bladder; C C, rectum; D, anterior, and E, posterior lip of cervix uteri; F, connective tissue uniting the anterior wall of the cervix to the bladder; G, lax tissue between the posterior wall of the cervix and the peritoneum; H, vagina.

* Zur Anatomie und Physiologie der Beckenorgane, von Dr. O. Kohlrausch, Leipzig, 1854.

be observed, this distinction in a great measure vanishes under the application of the microscope.

Peritoneal coat. — The outer serous coat, which constitutes the thinnest of the three component tissues of the uterus, is formed of the centre of the principal fold of the broad ligament, which is closely applied to the uterine body and fundus, and to a portion of its neck.

It is of great importance to the comprehension of certain points in the pathology of the uterus, to be hereafter considered, that the relations of this peritoneal covering to the proper structures of the organ, as well as to adjacent parts, should be accurately determined. The most important of these relations are shown in *fig.* 433., representing a vertical section of the pelvis and its contents. In this view the reflexions of peritoneum over the centre of the uterus are shown. The membrane, after lining the abdominal walls, and covering the fundus, and a portion of the posterior surface of the bladder, is suddenly arrested in its descent at a point very nearly opposite to, but sometimes a little below the internal os uteri, and therefore about the seat of junction of the body with the neck of the uterus. Here the membrane forms a sharp fold or angle, and becomes immediately applied to the anterior face of the uterine body, while the cervix, which lies in great part, if not entirely, below this level is left uninvested. The peritoneum, then, after ascending over the anterior uterine wall, covers the fundus and sides of the organ, and descending upon the posterior surface, it remains closely adherent to the tissues beneath, until it reaches the level of the anterior point of reflexion. At this point the peritoneum becomes much more loosely connected with the uterus by the interposition of a quantity of lax connective tissue which intervenes between it and the posterior cervical wall (*fig.* 433, G). The membrane, however, still descends, covering first the posterior wall of the supra-vaginal portion of the cervix, and then a part of the fornix, or upper end of the vagina. The extent of peritoneal covering which the vagina receives, varies in different subjects from half an inch to nearly an inch. The membrane then, as before, turns upwards, but at a more obtuse angle, to invest the rectum, so that a pouch is formed, termed the recto-vaginal or retro-uterine pouch, which is sometimes of considerable size.

The adhesion of the peritoneum to the uterus is closest along the median line, and over the whole of the fundus, at which points its separation by dissection from the tissues beneath cannot be effected without the aid of prolonged maceration; but towards either side of the organ the connection is less intimate, so that here the membrane may be made to glide to a limited extent over the sub-lying structures. At the two upper uterine angles the peritoneum is continued on to the uterine appendages; viz., the Fallopian tubes, round ligaments and ligaments of the ovaries. After sending off extensions to invest these parts, the portions of membrane which cover the anterior and posterior faces of the uterus respectively come nearly into apposition along the lateral borders of the organ (*fig.* 427.), where they are conjoined by a quantity of lax fibrous tissue, which serves to bind them loosely together, and at the same time to give support and protection to the numerous blood vessels entering the uterus on either side along the whole of this border.

A similar portion of lax fibrous tissue serves to connect the anterior wall of the uterine cervix, where it is uncovered by peritoneum with the posterior surface of the bladder, with which it lies in contact.

The sectional views of the uterus in three directions already given serve to explain the whole of the relations of the outer or peritoneal coat of the uterus to the muscular or proper coat.

Fig. 426. shows the mode of attachment of this membrane to the anterior and posterior surface and fundus along the median line, and also the parts which are left uncovered by peritoneum. Commencing from the os uteri the vaginal portion of the cervix forming the anterior lip (*a*) receives an investment of mucous membrane as far as its point of attachment to the anterior wall of the vagina (*v a*). Beyond this the whole of the remaining portion of the anterior wall of the cervix, measuring above one inch in length (*b b*), is left uncovered either by mucous or serous membrane. At the termination of this space the peritoneum, reflected off from the bladder, reaches the uterus, and after investing the organ, is continued down to and beyond the fornix of the vagina (*f*). But at this point the mass of loose connective tissue before referred to separates the peritoneum from the posterior cervical wall to a great extent (*c*), while finally a much larger portion of the cervix is contained within the vagina, posteriorly than anteriorly, and is consequently covered by mucous membrane (*p*), because the vaginal walls are attached at a much higher point here than anteriorly.

Fig. 431. serves to exhibit the relations of the peritoneum to the fundus, and the absence of that membrane from the lateral borders of the uterus, while *figs.* 427.—430. exhibit the relative proportions of the covered and uncovered parts as seen in a series of horizontal sections of different portions of the organ.

The middle or smooth-muscular coat, upon which depends the remarkable firmness and solidity of the uterus, constitutes the principal bulk of the organ. This coat upon section appears of a pale pink colour, mottled with irregular white lines, and permeated by vessels which are particularly numerous near its lateral borders. The following are the component tissues of the middle uterine coat, viz.:—

1st. *Smooth-muscular fibres.* — These are found in every portion of this coat, and consist of fusiform fibres of the kind termed by Kölliker contractile fibre-cells, in which a single elongated oval nucleus may be occasionally brought into view with difficulty. They all contain minute dark granules easily distinguished, and they sometimes exhibit upon their surface slight longitudinal folds or markings. These fibres have an average length of $\frac{1}{1000}''$, and breadth of $\frac{1}{6000}''$. They are deeply imbedded in the uterine substance from which they are with difficulty obtained separate, but they may be commonly seen projecting to the extent of about half their length from the torn margin of the preparation, and they are easily rendered

Fig. 434.

Smooth-muscular fibre of uterus.

a, fibres united by amorphous matrix; *b*, separate fibre and elementary corpuscles. (*Ad Nat.*)

visible in its substance by the aid of dilute acetic acid. These fibres do not apparently possess any distinct cell membrane. In very thin sections the ends of the fibres which have been transversely divided are seen as if solid, and the cut fibres do not collapse, nor have I ever been able to detect any appearance of a flowing out of fluid contents, which would be the case if the individual fibres consisted of a cell wall containing fluid (*fig.* 434. *a*).

2. *Round and oval nuclei, or elementary corpuscles.* — These measure $\frac{1}{6000}''$ in diameter. They are found in many parts intermixed with the fusiform fibres, but they are most abundant towards the inner layers of the muscular coat. They are apparently the elementary or embryonic condition of the fusiform fibre-cells just described. For although the two extreme forms of round corpuscles and fusiform fibres are the conditions under which these constituents of the muscular coat are most numerously seen, there may yet be traced a sufficient number of apparently intermediate stages to justify the conclusion that the one is but the embryo form of the other; the round corpuscles becoming at first oval, and then being lengthened out into the fusiform state (*fig.* 434. *b*).

3. *Amorphous or homogeneous connective tissue.* — A considerable portion of connective tissue exists in certain parts of the uterus in the unformed state, constituting a transparent matrix in which the fibre-cells and nuclei are embedded, and by which they are so intimately united together, as to render their isolation, even with the aid of nitric acid, a work of great difficulty. The fibre-cells and nuclei which form the innermost laminæ of the muscular coat, as well as the laminæ themselves, appear to have scarcely any other connecting medium but this, especially in young subjects, while in the middle and outermost laminæ a large portion of fibrillated tissue is added, and the amorphous substance uniting the individual fibres into bundles is proportionally less in quantity.

4. *Fibrillated connective tissue* (white fibrous tissue). This, as just stated, is found chiefly among the middle and outer muscular laminæ, serving here the purpose of a connecting medium between the several layers, and supporting the blood-vessels ramifying between them. The presence of this form of fibrous tissue is most readily exhibited by taking a thin perpendicular section from the outer muscular layer, and slightly drawing the laminæ asunder, after submitting the preparation to the action of acetic acid. The layers and bundles of muscular fibre, as shown in *fig.* 437., are then seen to be surrounded by, and imbedded in, a quantity of white fibrous tissue which conceals the fibre-cells, and renders the distinguishing of them difficult.

The fibres of this tissue have clear and sharp edges, appear to be of indefinite length, are independent of each other, and are clearly not mere foldings in an amorphous substance. Among them, however, and especially at the points where the laminæ are separated, are seen numerous thin flat transparent bundles, marked by deep longitudinal wavy lines, to which the above explanation of the cause of the appearance of wavy lines in this tissue which many physiologists have adopted might be more safely applied. Occasionally these wavy bundles exhibit an appearance of sharp curling lines, such as would indicate the intermixture of a small quantity of elastic tissue.

5. *Elastic fibrous tissue.*—The elastic form of fibrous tissue is also present in the uterus, as just stated, though not in great quantity. Besides the occasional presence of strongly curled fibres there may be seen in many places developed single fibres matted together, of the finer kind, commonly known as nucleus fibres; and also more abundantly the peculiar fusiform formative cells from which these arise. I have frequently had the opportunity of tracing these peculiar dark-bordered cells in process of transformation into the finer elastic fibres, and so far of confirming those views which ascribe to this form of fibre a cell origin.

These several tissues together with the uterine vessels and nerves, the former being in great quantity, make up the middle coat of the organ. And it is to the arrangement of these in laminæ and bundles which are separated from each other, and perforated as it were in all directions by numerous vascular channels, that the mottled appearance of the unimpregnated uterus, as seen in sections, is due.

The foregoing constituents of the middle uterine coat exist in different proportions in the body and neck of the organ respectively. In the body, notwithstanding the considerable amount of fibrous tissue by which the several component elements are connected together, the muscular fibre, either in its elementary or more developed condition, constitutes the largest portion, while in the cervix the fibrous element predominates, and the muscular fibre is proportionally less abundant.

Course of the muscular fibres. — Regarding the precise plan of arrangement of the constituent tissues of the middle uterine coat, and especially of its muscular element, in the unimpregnated state, numerous microscopic examinations have satisfied me that it is not possible to do more than to indicate these in a very general manner. Mme. Boivin attempted to describe the special course of the muscular fibres in the unimpregnated organ; but she appears to have abandoned the attempt after giving an account of what is seen upon the surface of the organ when the peritoneum has been stripped off after prolonged maceration. More recently the course of these fibres has been described by Kölliker, Gerlach, and others, in the deeper seated, as well as in the superficial layers.

In investigating this part of the subject it appears to me that a sufficient distinction has not been made between the course of the individual fibres, and the arrangement of the laminæ or bundles into which they are collected, for these are by no means necessarily the same.

According to my observations the contractile fibre-cells are not distributed in equal proportions through all parts of the muscular coat, nor are they found everywhere in the same condition. It has been already stated, that no strict line of demarcation is discernible by the microscope between the three several coats, of which the uterus is said to consist. And this is particularly the case in respect of the muscular fibres which permeate all of them. In the so-called mucous membrane the muscular fibre-cells are loosely arranged in an amorphous tissue, in which they lie embedded, intermixed with the elementary nuclear corpuscles, constituting their embryonic condition. Here the fibre-cells form bundles, situated between the ramified canals or utricular glands of the uterus, and take a direction more or less oblique or perpendicular with regard to the inner uterine surface. But at the level of the base of the uterine follicles, where the proper muscular coat is considered to begin, and the mucous membrane to terminate, the contractile fibre-cells assume a different direction and arrangement. Here at once they begin to exhibit a certain order of stratification, the strata being very closely superimposed, and arranged for the most part in such a manner as to lie parallel with the walls of the uterine cavity, which is therefore surrounded by them.

These strata exhibit certain differences of composition and arrangement sufficient, for the sake of description at least, to justify an artificial division of them into three orders.

The innermost of these may be termed the dense muscular strata. They commence immediately external to the mucous membrane, and extend outwardly through about half or two thirds of the thickness of the muscular coat.

When preparations that have been preserved in weak spirit, or those that have been finely injected, are examined by the naked eye, or with a hand lens, a peculiar mottled appearance is presented by sections of this part,

Fig. 435.

Thin section of a portion of the uterine walls, commencing from the peritoneum and extending inwards, showing the irregular course of the strata of uterine fibre, and the divided vessels between them. (*Ad Nat.*)

caused by the intermixture of numerous minute white lines ramifying within a darker substance, and dividing it into a multitude of small lozenge-shaped spaces. The whiter lines mark the course of the finer uterine vessels, together with the bundles of white fibrous tissue which accompany them. The browner lozenge-shaped spaces consist of the fusiform contractile fibre-cells, united together by amorphous tissue into short bundles, which by their superposition constitute the laminæ just mentioned. When horizontal sections are made of this portion of the muscular coat, such as are represented in *fig.* 428., these bundles or strata are seen to be arranged in a concentric manner, forming interrupted circles surrounding the uterine cavity. But this appearance must not be regarded as indicative of any corresponding direction of the muscular fibre-cells, within these bundles or laminæ, for all appearance of a concentric plan, as regards the fibres, at once vanishes under the use of the microscope.

Fig. 436., representing a fine section taken from the inner muscular laminæ, serves to exhibit the mode in which the contractile fibre-cells are arranged in this portion of the uterine walls. The individual fibres and embryonic corpuscles are imbedded in an amorphous substance (the unformed connective tissue already described), by which they are aggregated together, so as to form bundles and laminæ. In these strata the fibre-cells appear to remain distinct, and to be separated from each other by a distance not greater usually than their own diameters.

This is best shown in fine sections, previously prepared by acetic acid; but it should be observed, that as this agent causes the intermediate tissue to swell, the normal distances between the cells may, to a certain extent, be thus artificially increased. The relation of the fibre-cells to the uniting material is most clearly exhibited in those parts of the preparation where the knife has divided the fibres transversely to their long axes. Here the relation of these two structures to each other may be exemplified by that of the harder and softer ingredients in certain portions of those geological formations termed conglomerate.

Fig. 436.

Portion of uterine tissue from the internal muscular layers. (*Ad Nat.* × 150.)

At the points where the knife has cut the fibres obliquely, a corresponding change is observable in the outlines of the divided fibre-cells, which present in these bundles the figure of caudate cells, while in other places, where the course of the fibres has run parallel with the surface of the section, the fusiform outline of the entire length of the fibre is distinguishable.

All these varieties of direction are noticeable in *fig.* 436., in a portion of uterine tissue not more than $\frac{1}{50}''$ in diameter. The fibres which are here seen forming bundles and layers, run in some instances parallel with the surfaces of the laminæ, and in other places spread out fan-shaped, or incline towards each other, like the component fibrillæ of the penniform muscles. The bundles and layers of fibres are close-set and compact, and a comparatively small amount of developed or fibrillated connective tissue is found between or among these elements of the innermost strata of the muscular coat. The fibre-cells also are here apparently softer and more fleshy, and appear to be of newer formation than those forming the layers which lie nearer to the peritoneum.

External to and surrounding these may be distinguished a second order of strata, among which the primary and secondary ramifications of the principal uterine arteries and veins are freely distributed; so that sections taken from this region do not present the same compact appearance as those from the inner layers, but are seen to be everywhere permeated by vascular channels, which are particularly conspicuous in the multiparous uterus. These numerous vessels, ramifying among the muscular fibres, make the course of the latter very irregular. When the section has been made parallel with the broad ligament, the tortuous arteries, entering the uterine texture between the folds of the latter, may be often traced to a considerable depth among the laminæ; while sections made in an opposite direction more frequently exhibit the gaping orifices of these vessels, and of the divided veins surrounded by laminæ of muscular fibres, and of a more lax and fibrillated form of connective tissue, than is found among the inner strata. This intermixture of the larger uterine vessels with the muscular strata constitutes here a very characteristic feature, and hence these middle strata may be distinguished as the vascular laminæ of the muscular coat.

External to these again lie a series of thin sheet-like laminæ (*fig.* 437.), forming a tegumental stratum which does not entirely surround the organ, nor cover it in all its parts. It consists of 6—12 thin close-lying layers of fibres, whose course is parallel with the uterine surface; the most external laminæ being inseparable from the peritoneum by which they are covered. These flat, thin, layers are continuous with and extended upon and into the broad and round ligaments, the Fallopian tubes, and the ligaments of the ovary, from which they spread out fan-shaped over the fundus and upper portion of the anterior and posterior uterine walls; meeting at length in a central perpendicular raphé, in which a few longitudinal bundles may be generally seen.

These tegumental laminæ are composed almost entirely of fusiform fibres, with very few embryonic corpuscles. They are united together by a large proportion of strongly fibrillated connective tissue, which is, however, sufficiently lax to permit a certain amount of artificial separation of the laminæ.

Fig. 437.

Portion of uterine tissue from the external muscular layers close to the peritoneum. (*Ad Nat.* × 150.)

Within these laminæ the fibre-cells are arranged in a manner somewhat different from that which characterises the internal strata. The amount of amorphous connecting matrix is here so small that the fibre-cells lie apparently in close apposition, their extremities interdigitating with each other, so as to form an imbricated pattern (*fig.* 434.). These fibres do not so frequently change their course as the fibres of the innermost strata, but form a more continuous series; so that sections of this part of the muscular coat are easily obtained, exhibiting the appearance of longitudinal strata, or bundles of fibre, such as are represented in *fig.* 437. The course of the individual fibres within them is, however, traced with difficulty, on account of the large quantity of fibrillated connective tissue by which these layers are surrounded and conjoined.

Immediately beneath the peritoneum all the constituents of the muscular coat are condensed into a tissue which cannot be easily unravelled. Through this, however, numerous fibres may be seen to run in a direction more or less perpendicular to the surface, apparently for the purpose of connecting the peritoneum with the coat beneath.

The mucous or deciduous coat; Lining membrane of the cavity of the uterus.—This forms a moderately thick and soft layer which lines the entire cavity of the uterus, and is continuous with the lining membrane of the Fallopian tubes, and of the cervical canal. On account of the large supply of capillary vessels which it receives, the mucous membrane is usually distinguished from the rest of the uterine parietes by its brighter red colour. It presents also to the unaided eye, when horizontal sections are examined, an appearance of being thrown into minute folds running perpendicular to the uterine cavity (*fig.* 438.). These apparent foldings, however, are shown by a strong lens to consist of a series of ramified canals, which constitute the most remarkable peculiarity of this membrane. The proportionate thickness of the mucous membrane relatively to the rest of the uterine walls, though variable in respect of age and other circumstances, is usually about $\frac{1}{8}$th of their diameter. Its greatest thickness is found about the middle of the cavity, while towards the internal os uteri, and still more in the region of the fundus, the thickness is slightly diminished.

To the unaided eye, the mucous membrane lining the body of the uterus, when viewed from the uterine cavity, is apparently smooth, or is seen to be perforated by minute apertures, but it rarely presents the appearance of deep folds or plicæ such as are always found in the cavity of the cervix. Occasionally the surface is roughened and flocculent from the exfoliation of its epithelial covering. The appearance of minute perforations is then lost, and a tomentose or apparently villous condition of the surface occasioned by the loosening out and partial detachment of the capillaries which freely ramify within this membrane is observed.

The lining membrane of the uterus differs from mucous membranes in general in having no sub-mucous tissue, so that it cannot, like that of the intestines, be made to glide upon the sublying tissues, nor be dissected off from them so as to be displayed in a distinct layer. When very thin sections from spirit preparations are examined by transmitted light with a common lens, or with a low power of the microscope, the mucous is distinguishable from the muscular coat chiefly by its greater opacity and peculiar greyish colour, as well as by the numerous tortuous canals which permeate its substance, running chiefly in a direction perpendicular to the inner surface of the membrane, and strongly resembling in their general contour the cerebral convolutions.

Under the application of dilute acetic acid this comparative opacity and grey hue immediately disappear, and the tortuous canals alone serve to mark the boundary between the two coats. When an amplifying power sufficient to discriminate the component tissues is employed, the distinction between the two coats becomes still less apparent, because their constituent elements are then seen to pass from the one to the other by almost imperceptible gradations, the difference between them being then shown to be morphological rather than structural, at least, at the points of their confluence.

The mucous membrane lining the uterine cavity is composed of the following elements, besides the utricular glands, capillary vessels, and epithelium, viz., — free elementary corpuscles or nuclei, contractile fibre-cells, and amorphous connective tissue.

1. *Free elementary corpuscles or nuclei.* — These are in all respects precisely similar to the elementary corpuscles already described as constituting apparently the embryonic state of the contractile fibre-cells in the muscular coat. They form in conjunction with the amorphous matter the principal portion of the uterine lining membrane towards its inner surface. Here they are arranged in nearly close apposition, being imbedded in an amorphous blastema, yet not so closely as to cause any mutual disturbance of their round or oval forms.

2. *Fusiform fibres or contractile fibre-cells.* — In the account which has been already given of the muscular coat, the contractile fibres are described as existing in all the coats of the uterus. In the mucous membrane they are very abundant, especially towards the outer surface, or that part in which the muscular and mucous coats become conjoined, and where the transition from the one to the other is almost imperceptible, and is chiefly observable on account of the difference in the arrangement of the constituent tissues of each. The fusiform fibres of the mucous membrane are gathered into loose bundles, united by amorphous tissue and intermixed with the elementary corpuscles from which they are developed. These bundles, the form of which is sometimes like the head of an arrow, are usually found between the utricular glands, pointing in a direction perpendicular to the uterine cavity.

The individual fibres have here a softer, paler, and more fleshy aspect than in any other portion of the uterine coats; they are apparently the youngest and most newly formed of the muscular fibres composing the uterus.

3. *Amorphous connective tissue* constitutes the chief bond of union between the several elements of the uterine mucous coat, and enters largely into the composition of the utricular glands. It presents no special character requiring a more particular description than has been already given of it in the account of the muscular coat.

Utricular glands or follicles. — These structures, which were first more particularly described by E. H. Weber and Professor Sharpey, constitute the most remarkable characteristic of the uterine mucous membrane.

By Reichert *, who has also investigated the subject, they were found present in every mammal which he had examined. The uterine glands or follicles consist of involutions or depressions of the mucous membrane, which are exceedingly numerous, and lie tolerably close together. They generally present the form of canals taking their course from the muscular walls of the uterus, through the substance of the parenchyma of the mucous membrane towards its free surface, where they terminate each in a separate orifice.

In Ruminantia and Pachydermata they are large, and take a serpentine direction, so that they may be easily mistaken for vessels. By Burckhardt †, indeed, who has described them in the cow, they were termed vasa spiralia. Their spiral course is more obvious in the rodentia and carnivora. In the rabbit they are short and wide. The orifices by which the utricular glands terminate upon the surface of the mucous membrane are in some animals large enough to be distinguished by the naked eye, as, for example, in ruminants, and occasionally in man; but more frequently these require the aid of a lens for their detection.

In the dog, two sorts of glands are described by Professor Sharpey ‡, simple and compound. The simple glands, which are the more numerous, are merely very short unbranched tubes closed at one end; the compound glands have a long duct dividing

* The composition of the mucous membrane of the uterus has been carefully investigated by Robin and Reichert; vide Robin, "Mémoire pour servir à l'Histoire Anat. et Path. de la Memb. Muqueuse Utérine; Archiv. Gen. de Méd. iv. série, tom. xvii.; Reichert, Ueber die Bildung der hinfälligen Häute; Müller's Archiv für Anat. Phys. 1848.

† Observ. anat. de Uteri Vaccini Fabrica.

‡ Müller's Physiology, by Baly, 1837, p. 1574.

into convoluted branches; both open on the inner surface of the membrane by small round orifices, lined with epithelium, and set closely together.

In man the form of the uterine follicles is by no means so definite as in the dog; nor is it possible by any mode of dissection with which I am acquainted to isolate and display them separately.* They form in fact a system of tortuous canals ramifying in the substance of the mucous membrane, in which they seem as it were to be excavated. They are so closely set as apparently to possess no distinct boundary wall, but each canal is separated from those contiguous to it by a variable thickness of parenchyma, consisting chiefly of the elementary corpuscles and amorphous tissue just described, together with a certain admixture of fibre-cells, usually found near the basal ends of the glands. No section that I have ever made has succeeded in exhibiting even a single gland divided longitudinally in such a way as to lay open the canal in its entire length, but every section made perpendicular to the surface presents the same appearance of numerous close-set meandering canals laid open for short distances, and giving to the surfaces of the section an outline

Fig. 438.

Section of the entire thickness of the uterine mucous membrane (decidua) in the unimpregnated state, with a small portion of the muscular coat attached.

The pale tortuous lines exhibit the course of the canals, termed uterine glands, the darker intermediate substance forms their walls. The finer lines are the capillaries of the mucous membrane injected. (*Ad Nat.*)

exactly resembling the cerebral convolutions. On account of this peculiarity it is difficult to determine whether these so-called glands consist of single isolated canals, or of a series communicating with each other. For the same reason it is also difficult to ascertain the precise mode of their termination towards the muscular coat, whether in a blind extremity in every case, as Weber represents them, or whether by any indirect communication with the uterine vessels, which many considerations both physiological and pathological seem to point out as at least possible. The difficulties attending this part of the enquiry have been ably illustrated by Dr. Sharpey, and my own investigations fully confirm his statements upon this point. Nevertheless I have in many instances succeeded in distinctly observing the blind termination of these canals towards the muscular coat.*

When sections of the mucous membrane are made parallel with, instead of perpendicular to, the surface, these canals are seen divided across. The appearance then presented is that of numerous round or oval apertures, which are more distinct in proportion as the section is made nearer to the uterine cavity.

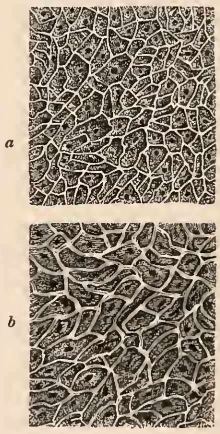
The uterine glands are lined by a fine dentate epithelium, the cells of which are only slightly coherent at their margins.

The orifices by which they terminate upon the surface of the uterine cavity vary in diameter from $\frac{1}{200}''$ to $\frac{1}{500}''$.

In addition to the glands or canals already described, there may be often observed intermixed with them short mucous crypts, or even closed follicles. These appear to have been little noticed in the uterine cavity, but they are very distinctly seen when accidentally distended by accumulation of fluid. They then constitute a variety of those growths, which in more advanced stages have been designated by Dr. Oldham channel polypi.

The arrangement of the *capillary vessels* of the uterine mucous membrane is peculiar and

Fig. 439.



Net-work of capillaries on the surface of the mucous membrane of the uterus.

a, from the body; *b*, from the canal leading to the Fallopian tube. In the centre of each of the meshes is the orifice of a uterine gland. (*Ad Nat.*)

characteristic. The capillaries, which are of large size, usually descend between the canals of the uterine glands, giving to them a few

* It appears to me that the well-known representations of the human uterine glands by E. H. Weber (Zusätze zur Lehre vom Baue und den Verricht der Geschlechtsorgane, Taf. viii. f. 4, 5.) are too definite, and should be regarded rather as diagrams than actual representations of what is seen in any mere section. Though it should be observed that these figures are taken from the pregnant uterus where the glands have enlarged and become more distinct.

* Upon this subject see further, p. 666.

small branches in their course. Having reached the surface of the mucous membrane they spread out into a meshwork of round oval and hexagonal spaces, in the centre of each of which may be usually observed the orifice of a uterine gland. This is most easily seen in the neighbourhood of the Fallopian tubes, where the capillary network and glandular orifices are usually arranged with greater regularity than in other portions of the uterine cavity.

In many places, however, the small vessels furnishing the capillaries of the mucous membrane may be seen in injected preparations, lying close beneath the surface with which they run parallel, and if the veins have been filled, one or two principal ones may be noticed on each half of the median line, running in the longitudinal direction, and communicating by short branches with the capillaries just mentioned, from which the blood is thus conveyed away through the muscular walls to the larger veins.

The network of capillaries thus formed lies very superficially with regard to the uterine surface. The layer of epithelium covering them, and the nuclear corpuscles and amorphous tissue supporting them, appear to have so little cohesion, and to form so slight a protection, that the vessels are often seen to be nearly bare, while in some instances the individual capillaries may be observed hanging out loose into the uterine cavity, and giving to its surface a villous appearance. This constitutes one of those conditions which have led many anatomists to assert, and more to deny, that the mucous membrane of the cavity of the uterus is furnished with true villi.

Structure and arrangement of the tissues composing the cervix. — The cervix is composed of nearly the same elements as those which form the body of the uterus, but they are differently proportioned and arranged in the two organs.

The cervix cannot be said to consist, like the body, of three coats. It receives a covering of peritoneum only upon its posterior surface, while the anterior wall, as well as the lateral borders, remain uninvested. With the exception, therefore, of this partial covering, the cervix consists of a muscular and a mucous coat only (*fig.* 426—431.).

Muscular coat of the cervix. — On account of the large admixture of fibrous tissue with the muscular element here existing, this might with almost as much propriety be called the fibrous coat of the cervix. The muscular element of the cervix consists of the same fusiform fibre-cells as in the body; but the elementary corpuscles are here scantily seen. The fibrous element consists of long detached fibrils or of bundles of fibres of white fibrous tissue intermixed with much unformed material of the same kind, but stronger and tougher than that which unites the constituents of the muscular and mucous coats of the uterine body.

These several tissues are arranged in a manner not materially different from the plan already described as observable in the body of the uterus. But the thin external strata which form the tegumental layers of the body are wanting in the cervix. There may, however, be distinguished an outer and more vascular, and an inner and more dense series of laminæ. The laminæ of the outer series are intermingled with numerous divisions of the cervical branches of the uterine vessels which traverse them obliquely in a direction from above downwards and from without inwards. From the abundance of these vessels the external laminæ present a more spongy appearance, and when the part has been injected a much deeper colour than the inner layers, which are paler, more dense and closely set, and exhibit at the same time fewer sections of vessels, and these only of the finer kind. The large amount of white fibrous tissue, and the density and compactness of the laminæ here formed around the cervical canal, give to clean sections of this part an appearance of circles concentrically arranged. But a low magnifying power is sufficient to resolve these into the lozenge-shaped spaces already described, consisting of bundles of contractile fibre cells bordered by fibrous tissue, and intermingled with bundles of the latter and blood-vessels of various sizes. Within these laminæ and bundles the fibres take their course with as many variations in direction and plan of arrangement as are noticeable in the muscular fibres of the rest of the uterus. (See *fig.* 436.)

The larger proportion of the fibrous element in the neck as compared with the body of the uterus, which the microscope serves to display, and which to a certain extent is observable to the naked eye, may be more satisfactorily shown by the operation of dilute acetic acid; this agent causing thin sections of the part rapidly to swell out and assume a gelatinous appearance.

Mucous coat of the cervix. — This is composed of epithelium, basement membrane, and the usual fibrous and vascular tissues, together with certain papillæ and follicles. It is of a more dense and uniform texture upon the outer or vaginal portion of the cervix than within the canal, where it is more delicate, but being here thrown into numerous folds and rugæ, an appearance is given of greater thickness than the membrane really possesses. The average thickness of the mucous membrane upon the lips of the cervix is $\frac{1}{2}$ — $\frac{1}{3}'''$; that of the membrane within the cervical canal, regardless of the folds, is somewhat less. The general plan of arrangement, and some of the more prominent forms which this membrane assumes within the cervical canal having been already considered, it only remains here to describe the minuter structures of which it consists.

The epithelium of the outer or vaginal portion of the cervix is tessellated or squamous. It gives a smooth and even covering to the two lips of which this part of the cervix consists. Outwardly, this scaly epithelium is continuous with that of the vagina, but towards the os uteri it terminates at the margin of either lip. Within the cervical canal the epithelium changes its form. It has been described here as constantly cylindrical or dentate; but upon all the finer structures here found, such as the filiform papillæ, this so-called epithelial covering consists, as Reichert has well described, and Kilian accurately represented it, of elementary cells, whose cell membranes are closely united together, having a polyhedral outline, and without undergoing such an amount of flattening as to lose their spherical form. They contain a slightly flattened nucleus with several nucleoli, surrounded by a clear somewhat thick fluid intermixed with molecular bodies, and sometimes oil globules.

Some difference of opinion exists as to the part of the cervical canal in which the epithelium first becomes ciliated. Drs. Tyler Smith, and Hassall, who have examined numerous uteri at an early period after death, with a view to anticipate post-mortem changes, state that the ciliation of the epithelium commences in the rugose portion of the canal, and extends up to the fundus, while the epithelium just within the os, though also cylindrical, is not ciliated.* It should be observed, however, that there is no particular portion of the cervical canal in which the membrane constantly becomes rugose, but that the rugosities often extend quite down to the margin of the os. According to Henle †, the cervix is provided with ciliated epithelium from the middle upwards, and with pavement epithelium from that point downwards.

One peculiarity or variety in the arrangement of the epithelium upon the vaginal portion of the cervix requires special notice here on account of the singular degree of importance which has of late years been attached to it, and still more from the remarkable pathological speculations to which it has given rise.

It occasionally happens that the tessellated epithelium of this part, instead of extending as far as the os, abruptly ceases at a distance of one or two lines from the inner margin of either or both lips, leaving a single or double crescentic patch where the ordinary pavement epithelium is replaced by a crop of close-set filiform papillæ, projecting very slightly, if at all, above the general surface, and presenting to the touch that velvety feel, and to the eye, on account of their great vascularity, that florid aspect, which has often led to the supposition that this mere morphological variety of structure is the result of a pathological change, and that it constitutes a form of ulcer peculiar to the os uteri.

Beneath the epithelium is a *basement membrane*, which, upon the outer portion of the cervix, extends in a smooth lamina over the papillæ that everywhere crowd this part, but within the cervical canal it dips into the furrows and follicles, or covers its numerous rugosities and projections.

An unequal layer of *fibrous tissue*, traversed by vessels, and supporting and containing the numerous papillæ and mucous crypts of various forms and sizes which characterise the cervical mucous membrane, completes this structure. Tough and coriaceous upon the outer portion, and thinner and more delicate within the canal of the cervix, it forms the chief substance of the mucous membrane, and lies immediately upon the muscular coat, the fibres of which become intermingled with it.

The papillæ, or villi, as they are sometimes termed, of the cervix, exhibit considerable varieties of size and figure, being conical, verrucose, or tuberculated, dentate, clavate, and filiform. The clavate papillæ are usually found fringing the surface and margins of the thinner plicæ. The dentate usually form a border to those which are a little more fleshy, and are commonly seen at the margins of the lateral and upper mucous folds. The verrucose papillæ are seen in various situations, but are most constantly observed in the sharp lateral furrows which constitute the lines of demarcation between the two cervical walls. The filiform papillæ are the finest of all. They are more slender and pointed than the clavate. They occur under two forms, and in two situations.

One of these forms is invariably present on the outer or vaginal part of the cervix. The whole of this portion, from the margins of the os outwardly, is covered by numerous short close-set thread-like papillæ, invisible to the naked eye, but with the help of a sufficient amplifying power easily distinguished by their white colour, through the somewhat dense layer of pavement epithelium and basement membrane that closely covers and binds them down. Similar papillæ clothe the inner surface of the vagina, and form, with those just described, a continuous layer.

The filiform papillæ constituting the second variety are larger and longer than these, so that they may be discerned by the naked eye. They occur usually at the margins of the os, and may be traced to a variable distance within the canal. But their presence here is uncertain, while that of the former variety is constant in the situations indicated. These larger filiform papillæ may be sometimes seen to form the terminations of the longitudinal cervical plicæ in those cases where parallel folds run down to the very margins of the os uteri. Here the folds, each ending in a little tuft or tassel, form by their junction a close-set crop of villi, which may merely border one or both lips with a narrow fringe, or form a velvetty patch extending outwardly upon the lips of the cervix, and being here uncovered by the ordinary dense epithelial layer of this region, which, as just stated, sometimes, terminates at this spot with an abrupt margin, they may present the appearance already described as simulating an ulcer.

Regarding the *minute structure and composi-*

* Memoir on the Pathology and Treatment of Leucorrhœa, based upon the microscopical anatomy of the os and cervix uteri.—Med. Chir. Trans., vol. xxxv. 1852.

† Allegem. Anatom., p. 246.

tion of the papillæ, all but the finer kinds may be viewed as consisting of the same elements as the mucous membrane itself, for they appear to be produced by mere notchings or indentations, extending more or less deeply into that membrane; they are, in fact, little more than repetitions of the plicæ and sulci upon a smaller scale, with a slight difference of form. They serve to extend the secreting surface, and possibly to expose a larger aggregate superficies of vascular and nervous tissues.

One or more long and slender blood-vessels may usually be traced from the muscular coat running into each papilla. These are sufficiently conspicuous in thin sections without the aid of injections. By the aid of the latter they may be seen to terminate in vascular loops upon the ends of the papillæ, just as similar vessels may be observed to form wavy coils upon the crests of the plicæ by which the cervix is lined.

The filiform papillæ, both larger and smaller, are more finely-constructed than the rest. They often end in a slightly bulbous extremity. Those upon the outer portion of the cervix are usually single, their length being from two to six times that of their breadth. The free uncovered filiform papillæ of the cervical canal and margins of the os are relatively much longer. These latter are commonly branched, and in conformation occasionally resemble the early villi of the chorion. Each villus, whether single or ramified, contains usually a single capillary loop, which returns upon itself, and at the base passes on to another villus. Covering the capillary loop is a delicate basement membrane, uniting together the clear granule-holding nucleated cells, which constitute the epithelial covering as well as the substance of the villi, and of which a description has been already given.

No nerves have been traced into the papillæ, though Kilian* is of opinion that they are specially tactile or sensitive structures, and from various circumstances to be hereafter considered, it will appear probable that they are connected with the special nervous attributes of the cervix. I am disposed, however, to regard the sensibilities of the cervix, such as they are, as resident chiefly in the filiform papillæ.

The *mucous crypts or follicles* of the cervix are, for the most part, simple depressions in the mucous membrane, although in certain situations they penetrate more deeply, and approach in form the ramified and tortuous canals of the uterine body. Scarcely any portion of the cervical canal is free from these follicles, which serve to increase the extent of mucous surface, and apparently to furnish the special secretions of this part. They not only fill all the interspaces between the primary and secondary folds, but they are dotted over the ridges and prominences of the cervical lining membrane in countless numbers, extending from the internal to near the external os uteri. They commonly cease at a short distance from the margins of the latter, where a smooth space is often observable in one or both cervical walls. But they may be sometimes perceived at the very border of the lower orifice, and when in such a case one or both lips are slightly everted, as for example in certain hypertrophies of the cervical lining membrane, this follicular portion becomes protruded, while its florid colour, limited by an abrupt margin of the unaltered and paler squamous epithelium here suddenly commencing, an appearance is produced which may also easily be confounded with an ulcer.

The mucous crypts seldom extend beyond the border of the os, except in the cases just quoted, when, in fact, the relative situation only of the parts is changed. A few, however, may be sometimes seen scattered at tolerably regular intervals over the vaginal portion of the cervix. They sometimes also occur here, as well as within the cervix, and even in the uterine cavity, in the form of closed vesicles containing an opaline fluid, and perhaps may be regarded as in some instances pathological new formations.

The cervical mucous crypts are lined by epithelium and basement membrane. They contain a small quantity of mucus, together with granule cells. Those upon and near the margins of the os uteri may be sometimes observed to contain short papillæ within their margin.

Blood Vessels of the Uterus.

The Arteries are derived from two sources, viz. from the internal iliac and the ovarian or spermatics.

The vessels supplied from the former source are termed the uterine arteries. These are two in number, one for each side. They arise from the anterior division of the internal iliacs, and proceeding downwards and inwards pass between the folds of the broad ligament to the neck of the uterus. Here they take an upward course along the lateral border of the organ, describing several flexuosities, and giving off, in succession, branches to the upper part of the vagina, the neck, body, and fundus of the uterus; the latter inosculating with the branches derived from the spermatics. Free inosculations also take place in the substance and upon the surface of the uterus between the branches of the two sides, so that the entire uterus may be injected from either set of vessels.

The branches derived from the spermatic or ovarian arteries also enter between the folds of the broad ligament, and inosculate with the superior divisions of the uterine vessels near the fundus of the organ.

When, after a successful injection, thin slices are cut from the substance of the uterus and dried, and afterwards placed in Canada balsam, the whole appears to be a mass of vessels; the arrangement of which, however, may be easily

* See a valuable paper by Franz M. Kilian, entitled, Die Structur des Uterus bei Thieren, in Henle and Pfeufer's Zeitschrift, IX. Bd.

observed by a hand lens or a low power of the microscope. Many of the arteries down to $\frac{1}{10}'''$ or $\frac{1}{15}'''$ in diameter are still seen to take a remarkable corkscrew course, with numerous very close spirals, especially in the outer half of the sections. Beyond these the vessels take a straighter course, and at length, in their finer divisions, run in parallel lines, sending off minute twigs at right angles, which cross the ultimate fibres of the tissue, in the manner peculiar to muscular structure.

When the finer vessels of the *body* of the uterus have reached the mucous membrane, they dip down between the walls of the canals, termed uterine glands, and spread out in a network of capillaries; the meshes of which surround the orifices of those canals in the manner delineated in *fig*. 439. *a* and *b*.; and from these the blood is again collected by the small superficial veins, the course of which is described at p. 637.

The arteries which supply the *cervix* penetrate that part in a direction downwards and inwards, pursuing the same corkscrew course until they have nearly reached the mucous surface, where they break up into finer vessels and capillaries, which ramify over the rugæ in lines more parallel than those of the uterine body. Both the arteries and capillaries of the cervix are far less numerous than those of the body of the uterus; and, indeed, the cervix generally in respect of its composition exhibits a lower degree of organisation than that of the principal portion of the organ, although it appears to receive the largest supply of nerves.

The *veins* of the uterus take a course corresponding with that of the arteries, and are distinguished by the same names. They are considerably longer and more numerous than the latter. They form along the sides of the uterus and within the folds of the broad ligament a very considerable plexus (the uterine plexus), which, together with the venous channels or sinuses ramifying in the uterine substance, are more conveniently examined in the gravid organ, where they undergo great enlargement. See *figs*. 444. 449. and 453., and the descriptions of these.

Lymphatics. — These vessels are far more easily examined in the gravid than in the unimpregnated uterus. They are very numerous, and are divided by Cruveilhier into two orders; the superficial, which lie immediately beneath the peritoneum; and the deep-seated, which ramify in several places in the substance of the uterine walls. The lymphatics of the cervix terminate in the pelvic and sacral glands. Those of the body of the uterus, after traversing the broad ligaments and uniting with the lymphatics proceeding from the Fallopian tubes, ovaries, and round ligaments, empty themselves in the glands situated in front of the aorta and vena cava.

Nerves. — The nerves which supply the uterus are derived partly from the spinal, but principally from the sympathetic system. According to the dissections of Dr. Snow Beck *, the nerves which compose the hypogastric plexus, consisting of gelatinous and tubular fibres derived from the lower part of the superior aortic plexus *, on approaching the neck of the uterus begin to separate, and on a level with the os uteri are joined by branches which accompany the superior hæmorrhoidal artery. The anterior portion of the hypogastric plexus, after receiving branches which accompany the iliac arteries, passes inwards by the broad ligament, and supplies the lower half of the uterus. These nerves, which are continuations of the hypogastric plexus, as they approach the body of the uterus separate, and each pursues a different distribution. They lose the plexiform character and form a number of distinct fine cords.

These nerves, like all the nerves supplied to the uterus, are chiefly composed of gelatinous fibres, although some tubular fibres accompany them; but they are few in number, and appear to be far from forming the essential element of the uterine nerves.

The middle portion of the uterus is supplied by a distinct branch from the inferior aortic plexus; which, without communicating with the hypogastric branches, passes to the upper part of the uterine body and then divides, to supply the part between the previously described branches and the Fallopian tube, sending also a branch to the ovary.

The fundus is supplied sometimes by a

* Phil. Trans., 1846, part ii. p. 219.

* According to Dr. Snow Beck, the white tubular fibres which enter, pass through, and emerge from the *semilunar ganglia*, are all derived from cerebro-spinal nerves through the medium of the *splanchnic nerve*, while none of the tubular fibres actually arise from the ganglia (as Bidder and Volkmann suppose). The same was found to obtain in every instance of sympathetic ganglia examined; the tubular fibres could always be traced to the white connecting cord between the spinal and sympathetic nerves, and thence to the branch of the spinal nerve from which it is derived. The gelatinous fibres, on the other hand, all take their origin in the corpuscles of the ganglia. In the white cords connecting the spinal and sympathetic nerves, commonly regarded as roots of the sympathetic, the tubular fibres composing these, on being traced back to the spinal cord, were found to be derived from the motor and sensitive roots in apparently equal proportions. The elements of the lower part of the *superior aortic plexus* resemble those which form the semilunar ganglia, viz. tubular fibres derived from the lumbar nerves, and gelatinous fibres from the sympathetic ganglia.

The *inferior aortic plexus* is a continuation of the branches from the plexus last described. These divide to form the two lateral hypogastric plexuses, and here a crossing of fibres of the opposite side takes place.

The *lateral hypogastric plexus* is composed of gelatinous and tubular fibres derived from the superior aortic plexus. The distribution of nerves to the uterus from this, their main source, is described in the text.

The *sacral nerves*, although they supply the vagina, clitoris, labia, sphincter and levator ani, bladder, and rectum, send no direct branches to the uterus; nor is there, according to this author, any anatomical evidence to support the supposition which some have entertained, that filaments derived from these nerves might by a circuitous route reach the uterus after their union with the *pelvic plexus*. Phil. Trans., 1846, part ii.

branch which proceeds from the renal plexus in company with the spermatic artery, and is distributed also to the ovary.

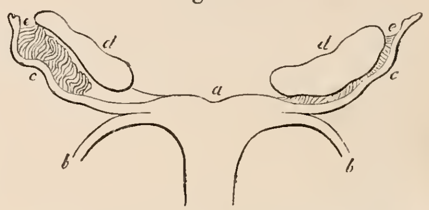
Another set, distinct from these nerves, comes also from the same continuation of the hypogastric plexus, but forms a plexiform arrangement around the vessels; and among these are found here and there minute ganglia. These nerves are very minute.*

The Development of the Uterus, and the Metamorphoses which it undergoes at Different Periods of Life.

a. The origin of the uterus, and its condition during fœtal life. — In the human embryo, according to the observations of Müller, during the transformation of the Wolffian bodies, the efferent tube of the generative apparatus undergoes the following modifications. In the male, all that portion of the efferent tube which passes along the outer border of the corpus Wolffianum is thrown into strongly marked convolutions, and this part contributes to the formation of the epididymis, while below this point the convolutions cease; and here a band or ligament, the gubernaculum testis of Hunter, which had been developed at a still earlier period, passes off to the inguinal canal. In the female, the following transformation occurs. The tube here remains free from convolutions, but a ligament, resembling that of the male, which is afterwards converted into the ligamentum uteri teres, passes off from the same point, to be extended to the inguinal ring. The part of the tube which lies below this point becomes the cornu uteri, and it is by the coalescence of the two cornua at their lower extremities that the body of the uterus is formed in man; while in those animals in which no middle portion or body exists, the cornua remain ununited. As the development of the uterus proceeds, the two cornua become gradually shorter, until at length they are lost, or, as it were, absorbed into the body or fundus of the uterus, which is thus at the same time developed.

The accompanying figure, representing the

Fig. 440.



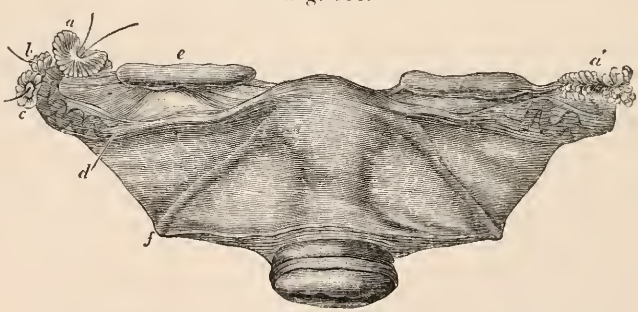
The entire internal generative organs, from a fœtus of three months. (After J. Müller × 8.)

a, uterus; *b*, round ligaments; *c*, Fallopian tubes; *d*, ovaries; *e*, remains of Wolffian bodies.

condition of the fœtal uterus at about the end of the third month of gestation, serves to illustrate these particulars. The ovaries possess the elongated form characteristic of the early condition of these organs. Parallel with them run the Fallopian tubes, and between these are the remains of the Wolffian bodies. At the point where the round ligaments are given off, the cornua uteri begin, and by their junction, which is here not yet complete, so that a slight indentation is left, the uterus is formed.

From this period of embryonic life, the uterus keeps pace in its growth with the other

Fig. 441.



Uterus and appendages of human fœtus at term. (After Richard.)

á, pavilion of the left side; *a*, the same of the right side (below it, in this specimen, is the remarkable variety of two separate accessory pavilions *b* and *c*); *d*, Fallopian tube, exhibiting numerous sinuosities in its outer half; *f*, round ligament; *e*, ovary.

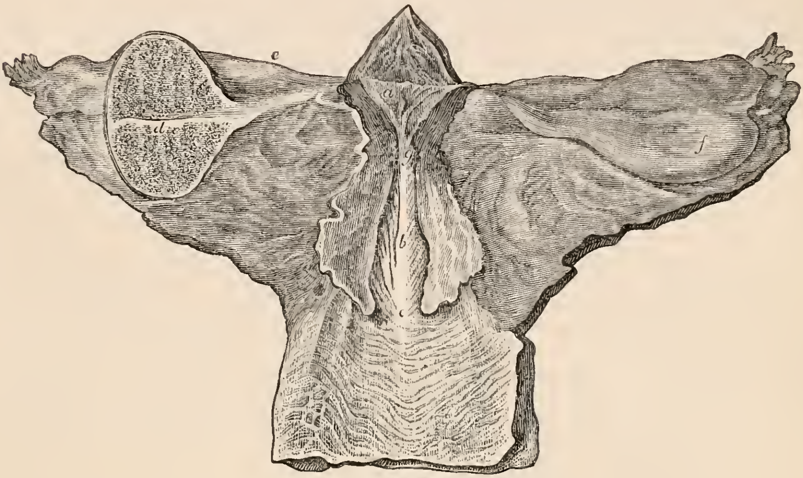
viscera; and at the time of birth it forms an organ of considerable size, lying high up in the pelvis, and occupying a conspicuous place midway between the bladder and rectum. The form, however, of the generative apparatus, at this stage of life, is very different from that which characterises it at a later period. The vagina, cervix, and body of the uterus constitute one nearly straight stem or canal, from which diverge, at right angles, the Fallopian tubes and ovaries with their ligaments, much in the form of the letter T. Of the two divisions of the uterus, viz. the body and cervix,

* Upon the subject of the origin and distribution of the uterine nerves, consult also Fr. Tiedemann; Tabulæ nervorum uteri, Heidelberg, 1822; and the works of Dr. Robert Lee, quoted at page 651., where the condition of these nerves in the gravid uterus, and the question of their enlargement during pregnancy, is considered. And for the minute anatomy of the sympathetic filaments and ganglia, see the Art. "Sympathetic Nerve."

the latter is the more considerable, for the body has not yet acquired breadth; while the cervix, forming a tube of nearly equal calibre with the body, possesses almost twice its length. This greater length of the cervix, as compared with the body of the uterus, is one of the most striking characteristics of fœtal life (*fig.* 441.), one also which continues to be observed for many years after birth.

b. The uterus from the time of birth to puberty.—From the time of birth until the approach of puberty, the internal generative organs undergo but little change. Gradually, but slowly, increasing in size, they still retain the principal characteristics of the fœtal period. The uterus consists still chiefly of cervix, the body being that part which is last developed. Thus in a child of three years (*fig.* 442.), in whom the entire length of the uterus is 15‴, the cervix measures 11‴, and

Fig. 442.



Uterus and appendages of an infant.

a, cavity of the body laid open; *b*, of the cervix; *c*, anterior lip of the cervix; *d*, left ovary opened; *e*, Fallopian tube; *f*, right ovary; *g*, internal os uteri, marking the division between the body and cervix. (*Ad Nat.*)

the body only 4‴. These dimensions do not materially differ from those of the uterus in the first year of life, nor do they much exceed those of the same organ at birth.

But as puberty approaches, the relative proportions of the cervix and body of the uterus are found to have changed, and the latter now preponderates over the former. For while the body now equals the cervix in length, the breadth of the former much exceeds that of the latter. The walls of the upper chamber now become thicker from the more rapid development of the uterine muscular fibre, which is their chief constituent. This not only increases the external dimensions of the organ, but, at the same time, causes the parietes to become incurved, and so to encroach upon the cavity contained by them, which, up to this period, preserves the form of a nearly equilateral triangle (*fig.* 442.), but now gradually acquires the shape already described as characteristic of the cavity of the adult uterus (*fig.* 431.).

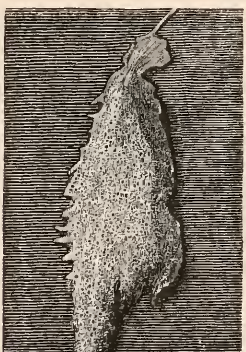
The folds or plicæ also (*fig.* 442.), which, in infantile life, are distinguishable upon the anterior and posterior walls of the cavity in the uterine body, resembling somewhat those in the cervical canal, gradually disappear; their former situation being now indicated by only a slight groove or raphé in the median line, and one or two gentle elevations diverging towards either Fallopian tube. These traces in the cavity of the body of its original construction out of two symmetrical halves, become generally lost after the uterus has been once impregnated, and indeed cannot always be distinctly seen in the nulliparous organ. One peculiarity in the form of the infantine uterus may be mentioned here, although it will be subsequently more particularly noticed. This consists in a curvature or inclination forwards of the upper part of the uterine body (*fig.* 467.). It is constantly more or less seen in infancy and childhood, and is usually partly retained in the virgin adult, but becomes lost after one or two pregnancies. In an excessive degree, it constitutes the condition hereafter described as antiflexion of the uterus.

From the time of birth to puberty, the component elements of the uterus remain nearly unchanged. They consist of granules and cells in various stages of development, from the round granular corpuscle to the elongated and ultimately fusiform fibre-cell; the two latter being often drawn out, at their extremities, into long filiform threads. These are all imbedded in a semitransparent formless matrix, and differ in no respect from the corresponding tissues in the adult, except that they are generally softer and less tenacious in proportion as they are younger.

c. The uterus during menstrual life. — The average duration of menstrual life is thirty years. It occupies usually the interval between the ages of fifteen and forty-five. The uterus in healthy women, throughout this entire epoch, is maintained in a state of perfect aptitude for the reproductive office, being, so to speak, under the control of the ovaries, with which it manifests so direct a sympathy, that every periodic change in the condition of the latter is, so far as the present state of our knowledge justifies the assertion, represented by a corresponding preparatory change in the former. But the menstrual phenomena being reserved for subsequent notice, it is only necessary to remark here that the uterus undergoes usually a slight alteration in size about the time of each catamenial flow, when its tissues are opened up, and become more spongy from the larger afflux of blood to them.

The lining membrane appears to suffer a variable amount of disintegration. In the uterus of women who have died during menstruation, the interior may present a slightly roughened appearance in certain places, or this may extend over the greater portion of the cavity. In women who menstruate painfully, it not infrequently happens that the entire uterine lining, to a greater or less depth, is exfoliated and discharged; the process of expulsion being accompanied by much suffering and a greater escape of blood than occurs in ordinary menstruation. These dysmenorrhœal membranes (*fig.* 443.) present all the charac-

Fig. 443.



*Portion of the lining membrane of the uterus cast off during painful menstruation. (Ad Nat.)**

teristics of a true decidual structure, having upon their inner side, or that which had corresponded with the uterine cavity, the fine cribriform surface occasioned by the orifices of numerous utricular glands, and upon the reverse side the usual rough flocculent appearance characteristic of the outer surface of membranes ordinarily discharged, along with the ovum, in abortion.

In other respects, the uterus, throughout menstrual life, exhibits little or no alteration in form or bulk, but continues to present those characteristics of constant aptitude for its greatest and most important office, which have been explained in the description already given of the adult organ; and these characteristics, if no pregnancy intervenes, it preserves until the period arrives at which menstruation, together with the capacity for procreation, finally ceases.

d. The uterus during gestation. The fully developed uterus. — The gravid uterus is only another term for the fully developed uterus; for, although the latter designation is commonly applied to the unimpregnated organ, when it has reached its ordinary size in the adult, the uterus does not attain the greatest amount of development of which it is normally susceptible until the term of gestation is complete.

The case of the uterus is perhaps in certain respects *sui generis;* for it is the case of an organ which, having reached a certain period of growth, remains in a nearly passive condition, so far as mere growth is concerned, until a further amount of development is evoked by a new stimulus. There are, indeed, two notable periods in the history of the development of the uterus, at which the influence of such an additional stimulus is perceptible.

For, first, as already shown, the uterus, like the mamma, remains without any material change from birth to puberty. The establishment of the latter condition is characterised by a correspondingly rapid evolution of both these organs. But the pubertal age may not arrive; the individual may retain, in respect of reproductive capacity, the pre-pubertal condition; and the uterus, in these cases, does not proceed beyond its first stage of development.*

Again, the second stage, having been reached at puberty, may be continued through menstrual life, until, with the cessation of procreative power, the period of natural decline in the organ commences, and this is the condition which the part retains during the periods or intervals when it is not employed in the process of reproduction, as well as throughout life in those cases in which it is never so employed. This degree of growth of the uterus is evoked by the full development of the ovary and the commencing discharge of ova, and is coexistent with the establishment of menstruation and the other conditions of puberty.

But a third stage of development of the uterus is produced normally by the stimulus of impregnation, and partly by the growth of the ovum, and abnormally by the formation of

* For this illustration I am indebted to Dr. Oldham.

* Compare *fig* 465., representing the pre-pubertal uterus in a woman aged nineteen, with *fig.* 442., of the uterus of a child at three years.

any substance within the uterus, such as a polypus, which may cause distension of its walls; or by the accumulation of fluid in its cavity, such as the menstrual fluid collected in cases of atresia or imperforation of the vagina.

The development of the uterus which is occasioned by the stimulus of pregnancy, takes place whether the impregnated ovum arrives within the uterine cavity or not; although this does not occur in equal degrees in the two cases. In the case of extra-uterine pregnancy, a very considerable thickening of the uterine substance usually takes place, together with a general enlargement of the entire organ, fully equal to that which is observed in the third month, and, in some cases, when gestation is not interrupted, even in the fourth month of ordinary pregnancy.

In cases where gestation follows an ordinary course, the development of the uterus is such, that the weight, at the end of the period, is found to be increased about twenty-four-fold, and its length about five-fold.

This development, as it affects the size, weight, form, and position of the entire organ, as well as the physical condition of its special parts, will now be considered.

There is no example in man, and few in the animal kingdom generally, of a development of any organ or structure comparable in rapidity with that which takes place in the uterus during gestation, although the periodical growth of the deer's horn, and the formation of the placenta, may be quoted as in some respects analogous cases.

Size. — The rate of increase of the uterus, during pregnancy, is subject to great variations. But, with due allowance for these, which are dependent chiefly upon the size of the fœtus and placenta, the quantity of liquor amnii, or the number of ova fertilised, an approximate estimate may be formed of the average alterations in size and bulk which the organ exhibits at different periods of normal gestation.

These may be expressed in calendar months as follows: —

RATE OF INCREASE IN SIZE OF THE GRAVID UTERUS ACCORDING TO MONTHS.

	Length.	Breadth.
End of 3 months	4½—5 inches	4 inches.
" 4 "	5½—6 "	5 "
" 5 "	6—7 "	5½ "
" 6 "	8—9 "	6½ "
" 7 "	10 "	7½ "
" 8 "	11 "	8 "
" 9 "	12 "	9 "

The antero-posterior has usually an average of one inch less than the lateral diameter.

Weight. — The weight of the gravid uterus, when fully developed, is most correctly ascertained in cases where death has taken place during, or soon after, labour at term. In twelve examples, estimated by Meckel, the minimum weight was 2lbs., and the weight, relatively to the unimpregnated organ, was as 24 to 1.*

Form. — The form of the uterus undergoes many changes in the course of gestation. During the first three months, although there is a considerable increase of size, the primitive figure is retained with only slight alterations. After the third month, the body rapidly enlarging, while the cervix remains nearly unaltered, the figure of the former approaches that of a sphere. For the perpendicular and transverse diameters of the body then become nearly equal, and the only deviation from the spherical form is occasioned, first, by the cervix, which increases the vertical diameter of the entire organ by one inch; and secondly, by the more tardy expansion of the body in the antero-posterior diameter, producing the form of a flattened sphere. After this, the perpendicular increasing more rapidly than the transverse diameter, and the upper segments widening faster than the lower ones, the uterus gradually acquires the ovoid figure which characterises it at the end of pregnancy.

Alterations, nearly corresponding with these, take place in the cavity of the uterine body. The walls of this flattened triangular chamber begin to separate from each other; and by their gradual expansion, the angles and superior and lateral lines, by which the cavity was at first bounded, are unfolded, so that the triangular is gradually exchanged for the pyriform shape, and this again for the figure of a flattened sphere — as in the fourth and fifth months of gestation; after which period the figure of the cavity corresponds very accurately with the general external form of the organ.

During these alterations, the fundus becomes strongly arched; while the sides undergo a slighter relative expansion, so that they exhibit only a gentle swelling; but the anterior and posterior walls become curved and prominent — sometimes the former, and sometimes the latter, according to Dr. W. Hunter, showing the greater amount of convexity.†

It has often been asked whether, during these changes, the walls of the uterus increase in thickness, or the contrary. In other words, whether the dilatation of the uterine cavity is to be regarded as a mere passive distension, with thinning of the walls; or whether the process of enlargement consists of an active excentric hypertrophy.

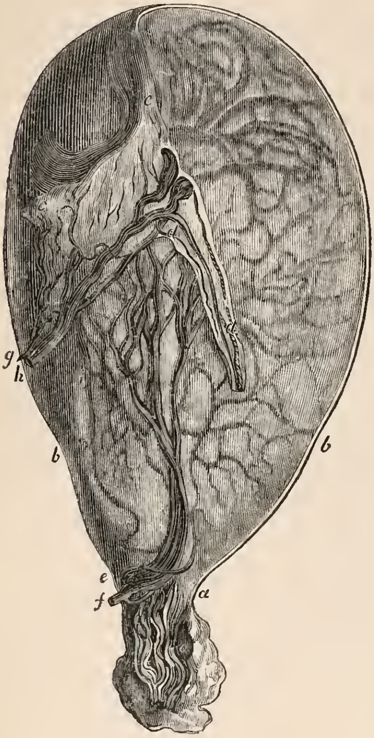
In order to determine this point, Meckel examined the average thickness of the uterine walls at different periods of gestation. From observations which he had made in sixteen uteri, at all periods of gestation, he concluded that the walls increase a little in thickness in the beginning, but that this increase is not very considerable, and that towards the end of pregnancy they become gradually much

* The estimates of Heschl, given at page 658., differ somewhat from these.

† W. Hunter. An anatomical description of the human gravid uterus, page 5.

thinner. He found the thickness of the uterine walls, three weeks after conception, $6'''$;

Fig. 444.



Human gravid uterus at eight months. The vessels have been injected, and the peritoneum removed from the sides and fore-part of the uterus. (*After Wm. Hunter.*)

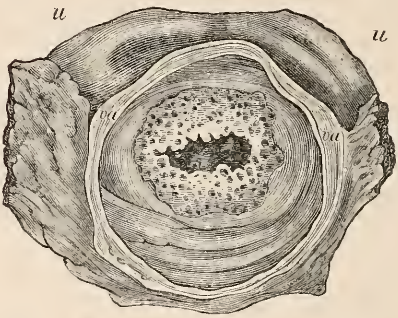
a, commencement of the cervix; *b b*, portion of the body corresponding with the brim of the pelvis; *c c*, Fallopian tube concealing the ovary; *d d*, round ligament; *e*, hypogastric artery, and *f*, vein; *g*, spermatic artery, and *h*, vein.

at the commencement of the third month, $5'''$; at the commencement of the fourth month, $4'''$. At the end of the fourth month, in two cases, $4'''$; in a third, $3'''$ at the upper, and $4'''$ at the lower part; in a fourth, $5'''$. At five months, in one case, $3'''$; in another, $2'''$ superiorly, and $4'''$ inferiorly. At six and seven months, rather less than $3'''$; at eight months, in one case, $2'''$, and $2\frac{1}{2}'''$; and in another, $3'''$ above, and more than $4'''$ below. At nine months, they appear to be still rather thinner.

In several uteri, which I have examined at all stages of gestation, I have found the thickness of the uterine walls exceedingly variable in different instances, even at corresponding periods of pregnancy, and particularly variable also in different parts of the same uterus.* According to my measurements, the extremes of thickness range from $2'''$ to $9'''$.

During these changes, which take place in the uterine body in the course of pregnancy, similar, but much slighter, alterations occur in the cervix. For the latter, being only the excretory channel of the uterus, undergoes no further modification than is necessary to prepare it for transmitting the fœtus when fully developed. Accordingly, in the early months of gestation, while the body is rapidly enlarging, the cervix undergoes but little change. Its tissues, however, become slightly expanded, so that the whole part is thicker, softer, and more elastic than in the virgin state. The margins of the os externum are consequently rendered more cushiony, and the orifice itself is enlarged. The canal of the cervix is also widened, and the palmæ plicatæ become unfolded, and project in the form of frill-like expansions (*fig.* 446.); while an unusual activity, occurring in the crypts and follicles, by which these parts are covered, a tough gelatinous secretion is poured out, which

Fig. 445.



Os and cervix uteri in the eighth month of pregnancy.

The os is surrounded by a broad disc of enlarged cervical follicles filled with a gelatinous secretion. The os is represented as seen from the vagina. *v a*, vaginal walls divided; *u*, walls of uterus. Half the natural size. (*Ad Nat.*)

collecting here in the form of a plug, assists in shutting out the uterine cavity and its contents from contact of external air and other influences.

The increase in size of the os and cervix, which is gradually progressive through the whole of gestation, will be sufficiently expressed by comparing the dimensions of these parts in their two extreme states. The virgin cervix measures usually at the base $7—8'''$ in its shorter, and $11—12'''$ in its transverse diameter, and has an aperture of $3—4'''$ wide. It projects into the vagina to the extent of $4'''$ (*fig.* 425). At the end of pregnancy, the whole vaginal portion of the cervix would fill a circle of $1\frac{1}{2}''$ diameter; the orifice measures transversely $10—11'''$; and that part which formerly projected into the fornix of the vagina, is now reduced nearly to the level of the vaginal walls.

During these changes, it is often observed, especially in a first pregnancy, that, as gestation advances, the projection of the cervix

* This circumstance is remarkably exemplified in prep. No. 3605, in the Museum of the Royal College of Surgeons, London.

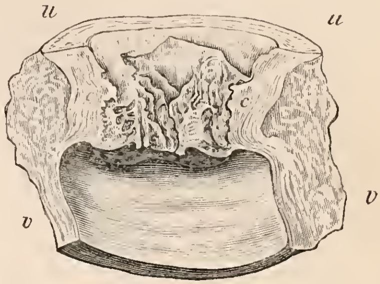
uteri into the upper part of the vagina becomes gradually less and less distinctly ascertainable by the finger. The latter change is commonly termed the "shortening of the cervix;" but the conditions upon which it depends, have not been very accurately examined, and they are certainly not at all clearly or adequately represented by the figures by which the description of this process is usually accompanied. As much importance is usually attached, in works on forensic and obstetric medicine, to the changes in question, it will be necessary here to examine a little more closely the process by which this apparent shortening of the cervix is produced.

It is commonly said that no material alteration, in the length of the cervix uteri, occurs before the fifth month of gestation; that, at the sixth or seventh month, the uterine neck has begun to shorten; at the eighth month, it is nearly, and at the end of the ninth month, it is quite, obliterated.

But while it is true that a lessening of the projection of the cervix into the vagina commonly takes place in pregnancy (*fig.* 446.), I can hardly coincide in the explanation which is usually offered of this circumstance, namely, that it is due to a gradual drawing up, as it were, of the cervix, by which its walls become added to those of the body of the uterus, for the purpose of increasing the capacity of the uterine cavity; and that in this way the uterine neck is gradually shortened, until it finally disappears.*

The accompanying *fig.* 446. exhibits the condition of the cervix in a woman aged thirty-seven, who, having previously borne children, died of phthisis in the eighth month of pregnancy. Here it will be perceived, that, without any actual diminution of the length of the cervix, which measured rather more than one inch, still there is no projection of it into the vagina; but that it forms a flat roof to that canal in the mode which is usually described and explained as indicating the entire absorption of the uterine neck. The true explanation of this, as it appears to me, is, that the apparent shortening of the neck is caused not, at first, by any diminution of its actual length, but by an increase of its breadth, or its extension in the lateral direction, whereby the projection of the lips into the vagina is reduced to the smallest possible amount. The rest of the process, upon which the shortening of the cervix depends, may be explained by the variable condition of the internal os uteri, or upper orifice of the cervix. If this remains unyielding until the time of labour,

Fig. 446.



Vertical section of the os and cervix uteri represented in the last figure.

v, walls of vagina; *c*, of cervix, and *u*, of uterine body. The cervical canal is nearly filled by the expanded palmæ plicatæ. Half the natural size. (*Ad Nat.*)

then the finger, on being placed within the cervix, traverses the whole length of the canal before it reaches any part of the child; and the general form and substance of the cervix being retained, the neck is said to be unobliterated. Such is usually the state of parts after repeated pregnancies. But if the internal or upper os yields readily, as it usually does in the more advanced stage of a first pregnancy, then the head of the child gradually settles down upon the lower orifice, pressing aside the soft and yielding wall of the cervix, which thus forms for it a shallow, cup-like, or funnel-shaped recess, that may be so far said to be added to the uterine cavity; and the finger, on passing within the os readily, touches the child, without having to traverse any length of cervix.

When, therefore, the term, shortening of the uterine neck, is employed, it should be understood to imply that change which takes place from the hypertrophy and lateral extension of the vaginal portion of the cervix, combined sometimes with a separation of the cervical walls from each other, occasioned by the descent of the head of the child; the degree of this descent being regulated by the amount of yielding of the internal os uteri. But it does not signify any alteration in the anatomical condition of the cervix and body of the uterus, which in every case retain their distinctive characteristics to the end of pregnancy: while the dilatation of the cervical canal is only an occasional occurrence, limited to the last stage of pregnancy, and having nothing to do with that apparent shortening which begins after the fifth month.

Position actual and relative. — The enlargement which the uterus undergoes during gestation, occasions of necessity very considerable alterations in its actual and relative position. On the occurrence of pregnancy, the organ, at first concealed within the pelvis, sinks, by its increased weight, lower than usual within that

* See description of the figures in Gooch: "An account of some of the most important diseases peculiar to woman," p. 212; and Beck's Elements of Medical Jurisprudence, 5th edit. p. 128.

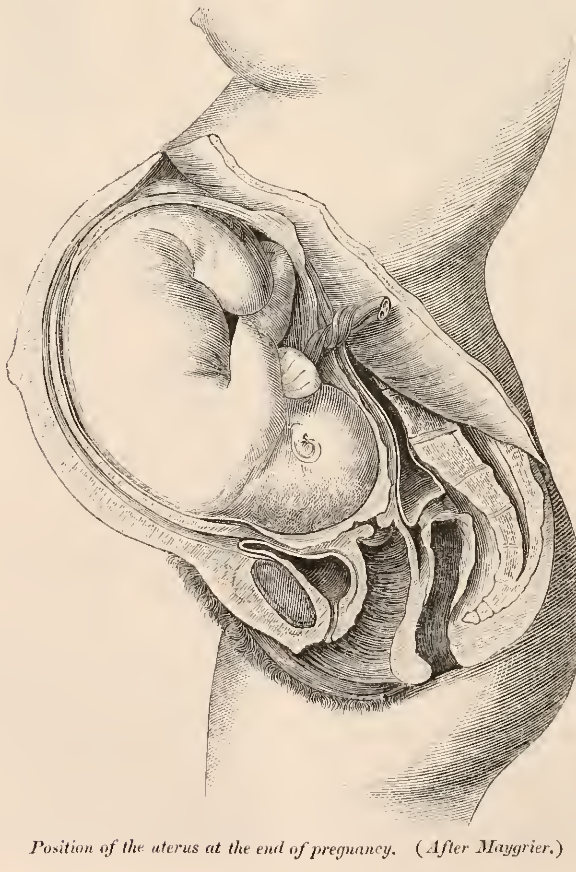
Regarding this explanation, which had been given by many preceding authors (see Mauriceau, tom. i. p. 97.; Smellie, vol. i. p. 183. *et seq.*), but which Gooch was, I believe, the first to illustrate by diagrams, it appears to me that much imagination has been exercised. The illustrations usually given are evidently diagrams supplied for the purpose of aiding the description of the process, as it has been supposed to occur, from examination of the part by the finger during life, but they give a very imperfect notion of the actual state of the cervix in pregnancy, as ascertained by dissection.

cavity; and, pressing upon the bladder and rectum, occasions sometimes an irritable condition of these parts. But usually at the end of the third month, the fundus may be felt emerging from the pelvic cavity; and in the course of the fourth month, it is always easily distinguishable in the lower part of the hypogastric region, having then risen to the height of about three fingers-breadth above the pelvic brim. In the fifth month, the hypogastric region is completely filled; the abdomen then acquiring a considerable rotundity in this situation. By the termination of the sixth month, the umbilical region also is filled, and the fundus uteri may be felt on a level with, or a little above, the navel. In the course of the remaining three months, the uterus rises gradually, until its fundus reaches the level of the ensiform cartilage. And this is very nearly the limit of its ascent, though it occasionally, and chiefly in first pregnancies, rises slightly above that point. In women who have a roomy pelvis, and in those cases where the natural form of the uterus is not altered by over-distension nor mal-position of the fœtus, there usually takes place, a few days or shortly before labour, a certain descent of the uterus, which has the effect of partially emptying the epigastric region, and relieving it from the pressure which it had sustained, especially during the last month.

The direction which the uterus takes in rising from the pelvis into the abdominal cavity, is determined by various circumstances; and it is interesting to observe in what way the addition of so large a body as the fully developed uterus to the already occupied abdomen, is provided for, without any of the viscera suffering injurious pressure, and without that impediment to the circulating and respiratory systems, which, in the absence of such a provision, must inevitably take place.

The oblique direction of the uterus, upwards and forwards, is determined, firstly, by the corresponding obliquity of the pelvis, the plane of whose brim forms with the horizon an angle of 60°. But as the fundus gradually, after three months, emerges from the pelvic cavity, the oblique direction of the uterus is maintained by the symphysis pubis in front, and the sacral promontory behind. Between these, the superior portion of the uterus continues to ascend, supported next by the abdominal walls anteriorly, and the spine posteriorly. The intestines, being bound down by the mesentery, cannot be displaced, and will

Fig. 447.



Position of the uterus at the end of pregnancy. (After Maygrier.)

therefore occupy a position midway between the spinal column and the posterior uterine wall. The pressure of the sacral promontory, and of the lumbar vertebræ, will still give to the uterus a forward tendency, which, on the other hand, will be prevented from becoming excessive by the elasticity of the front walls of the abdomen. If these have not been previously much distended, the fundus glides upwards, and ultimately fills the epigastric hollow; but if the abdominal walls have been much relaxed, as by frequent child-bearing, or if the pelvis is much deformed, the fundus uteri is usually turned directly forwards, or even downwards.

At the end of pregnancy, the whole of the fore part of the abdomen is occupied by the uterus; on either side lie the ascending and descending colon; the transverse arch, together with the omentum and stomach, fill the space between the fundus of the uterus and the diaphragm, while the rest of the abdominal viscera lie laterally and posteriorly to its hinder wall.

Thus it results, that in pregnancy, and especially in its last stages, no injurious pressure is exercised, either upon the great vessels, the aorta and vena cava, or upon the intestines, liver, or stomach, whilst the descent of the diaphragm, and, consequently, the act of respiration, is not materially impeded, and space is left for the bladder and rectum to perform their appropriate acts.

The situation and direction of the pregnant cervix, are necessarily affected by the increase of the principal organ, as well as by its contents. So long as the weight of the uterus causes it to descend lower into the pelvic cavity, as in the second and third months, the cervix is more readily reached, lying in the lower part of the hollow of the sacrum; but when the greater part of the uterus lies, as it does at a more advanced period, above the pelvic brim, the cervix is felt with greater difficulty, being more withdrawn from the entrance of the vagina. If the lower segment of the uterus is more than usually spread out, as in transverse presentations, or in the case of twins, or of excessive distension by liquor amnii, then the cervix and os are drawn up so high as sometimes to be quite beyond the reach of an ordinary finger; or, if the pelvis is very narrow, or the abdominal walls so lax as to cause the falling forward of the womb, the cervix will be equally beyond reach, and in these cases no part of the uterus can be said to be within the pelvic cavity. On the other hand, where the pelvis is unusually roomy, and the vagina and ligaments are lax, the cervix may lie immediately upon the perineum, or even project beyond the orifice of the vulva. In most cases the cervix lies lowest in the pelvis at the earlier and latter periods of pregnancy, and highest about and after the time of quickening. Its projection into the vagina is not always in the direction of the median line, but is more often inclined to the left side, as that of the fundus is towards the right. This obliquity in the position of the uterus may be caused by an unequal length of the ligaments, or more commonly by the projection of the lumbar vertebræ, which naturally gives to the body of the organ an inclination towards one or other side.

Alterations in the special coats and tissues.—*The Peritoneum* is that coat which suffers the least alteration during pregnancy, yet the changes which it exhibits are not inconsiderable. They consist chiefly in a simple multiplication of the component elements of the tissue, whereby it is enabled to keep pace with the enormous rate of growth of the uterus, so as still to invest all those portions which were covered by peritoneum in the unimpregnated state. During this process of growth, the membrane does not become attenuated, as would be the case if it suffered mere distension, but its thickness is rather increased, so that the addition of new matter must be in the aggregate very great.

Dr. W. Hunter imagined that this investment of the gravid uterus was accomplished by an unfolding of the layers of the broad ligament, for he asserts that, "in proportion as the circumference of the uterus grows larger, the broad ligaments grow narrower, their posterior lamella covering the posterior surface, and their anterior lamella covering the anterior surface of the uterus itself." He arrived at this conclusion from observing the altered relative situation of the appendages, and their appearance of clinging to the sides of the uterus in advanced stages of pregnancy. But the latter circumstance is due to the arching of the fundus, already described, which gives to the appendages a downward direction; while that the broad ligament does not disappear, as Dr. Hunter asserts, may be shown by measuring the alæ, or cutting them off, and comparing them with the same parts in the unimpregnated state, when little or no difference in respect of dimensions will be found between them in the two conditions.

Beneath the peritoneum of the gravid uterus is always found a large development of strong *fibrous tissue*, arranged in irregular cords and bundles. These sub-peritoneal fibres serve to strengthen the coats, and probably greatly contribute to prevent rupture of the organ, especially during labour.

The muscular or middle coat.—The tissues of which this coat is composed, together with their mode of arrangement in the unimpregnated uterus, have been already fully described. And it is to an increase of these, but especially of the vascular and muscular elements, that the enormous growth of the uterus during pregnancy is chiefly due. This growth consists partly in a greater development of the already existing structures, and partly in new formations.

The growth of the contractile fibre cells is here of especial interest. The elements of this tissue have been shown to consist, from infancy onwards, of fusiform fibre cells, intermixed with the round, oval, and elongated nuclei (*fig.* 434.), which constitute their embryonic condition. These, up to the time of impregnation, form the special and sole elements of the muscular tissue; yet some physiologists even of the present day refuse to recognise in these a muscular character, although it is plain that the uterus so constructed has a contractile power. The occurrence of abortion, sometimes at the very beginning of pregnancy, the expulsion of polypi and dysmenorrhœal membranes, and the painful contractions termed uterine colic, prove that the unimpregnated uterus is so endowed. This non-recognition of a muscular character in the uterus before pregnancy has arisen from the minute size of the individual fibres, and from the difficulty of explaining why these should grow to a given point, and then cease to be developed. But F. M. Kilian has given a happy illustration of this point, derived from the observation of Kölliker, that the contractile fibre cells which are found in the coats of the smaller blood-vessels, preserve a relative proportionate size to those of the larger ones, wherein they are more fully developed. So also the contractile fibre cells of the uterus proceed to a certain point of development in the unimpregnated organ, and there stop. And in this respect it makes little or no difference whether the organ examined has been taken from an infant or an adult.

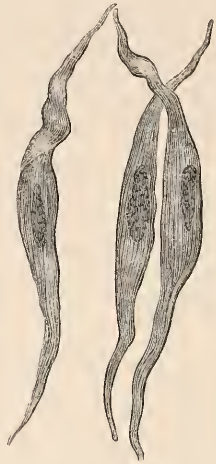
But when pregnancy takes place, the fibres proceed to a further stage of development. Their growth is now so considerable, that the contractile fibre cells, instead of a length of 0·002—0·003‴, and width of 0·002‴, in the fifth month, present a length of 0·06—0·12‴, and width of 0·0025—0·006‴, or even 0·01‴, and in the second half of the sixth month, a length of 0·1—0·25‴, a width of 0·004—0·005‴, and a thickness of 0·002—0·0028‴; consequently their length is increased from seven to eleven times, and their width from twice to five times.*

But in addition to this greater development of pre-existing fibre cells, a new formation of muscular fibre also takes place. This is observed, according to Kölliker, chiefly in the inner layers, although it may also occur in the external ones. The time of this new formation is chiefly the first half of pregnancy, the earlier forms of the fibre cells being no longer discernible after the twenty-sixth week. From this time onwards, the muscular coat contains only colossal fibre cells.

According to my observations, the individual fibre cells increase gradually in breadth throughout pregnancy, but their length is so variable, that the measurements just given can only be regarded as examples. The length, indeed, of the greater number of fibre cells after the third month cannot be determined with exactitude. A great many are thrown into numerous folds and contortions. Some exhibit transverse wrinkles, and the majority, when unbroken, end in long drawn out filaments, whose terminations become intermingled with the adjacent cells. Fine longitudinal markings are often distinguishable, and some fibres exhibit an elongated nucleus. The interior of the fibre is finely granular, and the margins show often a sinuous outline.

* Kölliker, Manual of Human Histology, Syd. Soc. vol. ii. p. 259.; and Siebold and Kölliker's Zeitschrift, 1848, bd. I. p. 72.

Fig. 448.

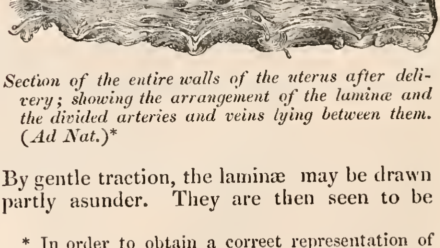


Fibre cells of gravid uterus fully developed. (*After Wagner.*)

The fibrous tissue uniting the several layers of muscles appears also to increase considerably, and towards the end of pregnancy to exhibit a distinct fibrillation.

These muscular and fibrous elements of the gravid uterus are arranged in numerous thin lamellæ, a good view of which may be obtained by cutting a thin slice perpendicularly out of the walls of the uterus at term.

Fig. 449.



Section of the entire walls of the uterus after delivery; showing the arrangement of the laminæ and the divided arteries and veins lying between them. (*Ad Nat.*)*

By gentle traction, the laminæ may be drawn partly asunder. They are then seen to be

* In order to obtain a correct representation of the course of the laminæ, I have here pinned out the preparation under spirit, and afterwards photographed it for engraving, of the natural size. By the stretching, the breadth of the preparation is doubled, and the laminæ are separated and rendered more distinct.

most densely and closely united towards the inner and outer surfaces, but to be more easily separable in the centre or vascular layer, where the laminæ are connected by a looser fibrous tissue, and are everywhere permeated by numerous large and small venous canals. These laminæ are superimposed the one upon the other, in layers parallel with the two surfaces of the uterine walls, but neither the laminæ themselves, nor the fibres composing them, can be said to take any definite course. Within the laminæ the fibres are arranged in flat bundles, which cross in all directions, as in the unimpregnated organ, but can seldom be traced in the same direction for any considerable distance. This is especially the case in the middle or vascular layer. In the superficial laminæ, the tendency of the fibres is to converge towards the angles to which the appendages are attached, while internally an apparent disposition to the formation of concentric circles around the orifices of the Fallopian tubes has been sometimes observed upon inverting the organ after labour. But nothing like a continuous arrangement of muscular fibres in the form of circular or longitudinal bands surrounding or investing the organ, can anywhere be demonstrated by the aid of the microscope.

The blood-vessels of the uterus undergo a marked increase in length, and especially in breadth, during pregnancy. The arteries pursue a remarkable spiral course whilst traversing the uterine walls. The veins form flattened channels between the muscular laminæ. The enlargement of the latter is accompanied partly by a growth of the muscular fibre cells already existing in their *tunica media* before pregnancy, and partly by a transformation of their inner and outer coats. Kölliker has observed, that in the fifth and sixth month, the fibres of the middle coat undergo an enlargement as considerable as those of the uterine walls, so that between these two scarcely any difference can be discerned. But besides these, both the inner coat, from the epithelium outwards, and the outer coat, acquire muscular fibres, which, except that they take a longitudinal direction, do not otherwise differ from those of the middle coat. This structure is found in the trunks of the uterine veins within the broad ligament, in the internal spermatics, and in all the veins of the uterine substances, which exceed 2‴ in diameter. In the smaller veins the muscular layer becomes less developed. Still, in those of ⅓‴ in diameter, a longitudinal layer of muscular fibre next the epithelium may be found. The only exceptions consist of those veins which, in the placental region, penetrate the inner layers of the uterus, to become continuous with the maternal veins of the placenta. These, notwithstanding their great width, instead of containing three, possess only one layer of muscular fibre, which, together with the epithelium, composes the entire coat of the vein.*

* Siebold and Kölliker's Zeitschrift, *loc. cit.* p. 81.

Do the nerves of the uterus enlarge or multiply during pregnancy?—This question, which once excited much controversy, has lost its chief physiological interest, since it has been determined that if any enlargement of the uterine nerves take place during pregnancy, this is nearly or entirely confined to the neurilemma, or fibrous nerve sheaths. Upon this point all observers are nearly or entirely agreed. Dr. Robert Lee states*, that whilst engaged in making dissections of the gravid uterus, he "discovered that the neurilemma was the constituent tissue of the ganglia and nerves which chiefly enlarged during pregnancy." Dr. Hirschfeld remarks, "this increase of volume does not occur in the nervous tubules, but in the neurilemma." M. Jobert de Lamballe having traced the nerves of the uterus in man and animals, both in the unimpregnated and gravid state, says, that he "never observed any modification of their physical condition. They appeared more voluminous in consequence of an infiltration of the cellular tissue which surrounds them, but they had not undergone any actual enlargement." Dr. Snow Beck removed the neurilemma, leaving only the bundles of nerve fibres or nerve tubules. On comparing the nerves of the gravid uterus with those of the unimpregnated organ, both dissections having been similarly conducted, he found that "the size of the nerves in both dissections is essentially the same; and when the nerves are carefully compared, no doubt is left that the nerves of the gravid uterus have undergone no change in size, nor any change in position, except that consequent upon the development of the organ."

But the neurilemma consists entirely of fibrous tissue, such as is common to most other parts of the body. It exhibits no structures specially nervous. Its offices, in relation to nerves and ganglia, are to support, protect, and bind together the nerve tubules and ganglionic nerve corpuscles.

Now the real point of interest to be determined is, whether during pregnancy the innervation of the uterus is increased in any degree proportionate to the augmented supply of blood to the organ. But the neurilemma has never been regarded as either a generator

* The Lancet, No. xvii. vol. ii. 1854, p. 349. Upon the subject of the nerves of the gravid uterus consult also, by the same author, "The Anatomy of the Nerves of the Uterus," 1841; "On the Nervous Ganglia of the Uterus," Philosophical Transactions, 1841, Part ii. p. 269.; 1842, Part ii. p. 173.; and 1846, Part ii. p. 211.; "Memoirs on the Ganglia and Nerves of the Uterus," 1849; and papers in the Lancet, vol. ii. 1854. Also the following:—Dr. Snow Beck, Philosophical Transactions, 1846, Part ii. p. 213.; and Papers in the Lancet, vol. ii. 1856; Jobert de Lamballe, "Recherches sur la disposition des Nerfs de l'Utérus," Comptes Rendus, 1841, p. 882.; F. M. Kilian, "Die Nerven des Uterus"; Zeitschrift, für Rat. Med., Henle und Pfeufer, Bd. X. 1851; M. Hirschfeld, "Note sur les Nerfs de l'Utérus;" Gazette Médicale, Oct. 1852, No. 44.; C. F. J. Boullard, M.D., "Quelques mots sur l'Utérus," 1853.

or conductor of nerve force, the former property belonging exclusively to the nerve centres, and the latter to the nerve tubes or nerve fibres. It is therefore necessary to ascertain if either nerve centres or nerve fibres become in any way multiplied or enlarged during the process of utero-gestation.

Regarding a new formation of nerve centres, there is at present no anatomical proof that any fresh ganglionic corpuscles are formed during pregnancy within the ganglia or plexuses from which nerves proceed to the uterine tissues.

Regarding the changes which take place in the nerve tubes or fibres during gestation, much interesting information is obtained from the researches of the late Dr. Franz M. Kilian, who devoted a considerable time to the investigation of this point. Dr. Kilian discovered, that in the unimpregnated uterus a successive diminution of the nerve fibre, whether in bundles or isolated, takes place as it approaches the point of distribution. If broad, the fibre, after a certain portion of its course, begins to lose its greater breadth, distinct double contour, and strongly marked granular contents, and then continuing as a pale fibre of intermediate size until it approaches nearer to the uterus, it ultimately assumes an embryonic character; that is, the extremely attenuated pale-margined fibre which traverses the tissues as a slender transparent band, has ceased to form a cylinder filled with nerve granules, and constitutes now only a pale slender stripe, or empty non-medullated sheath. Within this empty sheath there still occur, at distant intervals, little collections of granular fatty contents.

Now, in the early periods of pregnancy these embryonal forms are observed to become gradually more distinct between the muscular fibres, and at a later period many of the fine tubes become filled with medulla, which was wanting in the unimpregnated condition; the little collections of granular fatty contents just mentioned constituting the commencement of the nerve cylinders. For it is by the confluence of these isolated drops within the sheath that the medullated cylinder is formed, so that medullated fibres not only proceed as far as the uterus, but also become developed with continually increasing distinctness during pregnancy between the muscular fibres.

These observations correspond exactly with changes which Kilian observed to take place also in young animals, when the nerve fibres in the neighbourhood of the uterus are all in the embryonic condition, but become gradually medullated up to a certain point, in proportion as the development of the animal proceeds, so that the nerves may be said to grow forward in the direction of the uterus.

It should be understood, however, that in all these cases, the dimension of the nerve fibre never exceeds that of the branch whence it is derived, but that, on the contrary, a law of gradual diminution of the nerve is found to obtain in all cases, although the changes now described cause the rate of this to be different in the unimpregnated and gravid uterus respectively.

Kilian had no opportunity of examining the condition of the nerves in the human uterus at different periods of pregnancy, but he doubts not that the alterations are analogous to those which he found in animals.

The lining membrane of the uterus. Development of the decidua.— The last, and at the same time the most interesting, transformation of the uterine tissues remains to be described. It is that which takes place in the lining membrane, and which has for its object the formation of an immediate covering and protection to the ovum. By the aid of this membrane, the fertilised ovum, on arriving loose in the uterine cavity, is re-attached to the parent body, and is enabled to receive from it the supplies necessary for nutrition and growth.

But before the ovum enters the cavity of the uterus, the lining membrane of the latter swells and becomes softer and at the same time more vascular.* This augmentation in bulk of the uterine inner coat takes place in almost all cases when an ovum has been fertilised. That it does not depend upon the presence of the ovum in the uterus, is proved by the fact, that in cases of extra-uterine gestation, with rare exceptions, a development of decidua occurs within the uterus, forming there, in some cases, a more profuse growth even, relatively to the size of the uterus, than takes place in ordinary gestation.

The phenomena which ensue immediately

* In a paper on the Structure of the Placenta, by John Hunter, published in 1786 (Animal Economy), the decidua is described as composed of *coagulable lymph*. In another paper, 1794, on "the case of a young woman who poisoned herself in the first month of pregnancy," the pulpy substance lining the uterus, into which the blood-vessels of the uterus passed, and upon which they ramified, is stated to have consisted evidently of *blood coagulated*. The statements and descriptions in these two papers constitute the basis of the Hunterian hypothesis regarding the source of the decidua. But Dr. William Hunter had, even at that early period, a clearer perception of what the decidua really was, for in his posthumous work entitled "An Anatomical Description of the Human Gravid Uterus," edited by Dr. M. Baillie in 1794, the decidua is described in the following phrases: — "This membrane is an efflorescence of the internal coat of the uterus itself." . . . "It may be said to be the internal membrane of the uterus." . . . "It is really the internal lamella of the uterus." That the decidua constitutes simply a higher stage of development of the lining membrane of the unimpregnated uterus, in the same way that the muscular coat of the gravid organ is only a more advanced condition of the same coat before impregnation, is now proved beyond question. Upon this subject consult, in addition to the works quoted at p. 636., Sharpey, in "Müller's Physiology, by Baly," 1837, p. 1574.; Eschricht, "De Organis quæ Respirationi et Nutritioni Fœtus Mammalium inserviunt," 1837; F. M. Kilian, "Die Structur des Uterus bei Thieren," in Henle and Pfeufer's Zeitschrift, bd. ix.; Schrœder van der Kolk, "Waarnemingen over Het Maaksel van de Menschelijke Placenta;" and Coste, "Histoire Générale et Particulière du Développement des Corps Organisés."

upon the arrival of the ovum within the uterine cavity are, in the human subject, as yet unknown. Direct observation of the earliest stages are still wanting, and, unfortunately, the difference between these first steps in the mammalia (except Quadrumana) and man is so considerable, that only a limited aid can be derived from comparative observation. The ovum, when first found in the human uterus, is lodged in a small closed cavity, forming a continuous structure with the decidua which lines the rest of the uterine walls. In this little chamber, which may be formed at any part, but is most frequently seen near one or other of the tubal orifices, the little spherical ovum lies loose and unattached. In various examples which have been preserved and figured by different authors of the decidua at this stage, the size of this chamber varies from that of a pea to a hazel nut, and this size it acquires in the second week.

The walls of the cavity containing the ovum, and those forming the lining membrane of the uterus, are nearly alike in appearance and texture. They both consist of decidua, the former constituting the *decidua reflexa*, the latter the *decidua vera* of Dr. W. Hunter. For greater distinctness, those names are sometimes exchanged for *decidua chorii* or *ovuli*, and *decidua uteri*. The latter, according to a suggestion of Dr. M. Baillie, is also occasionally termed *parietal decidua*.

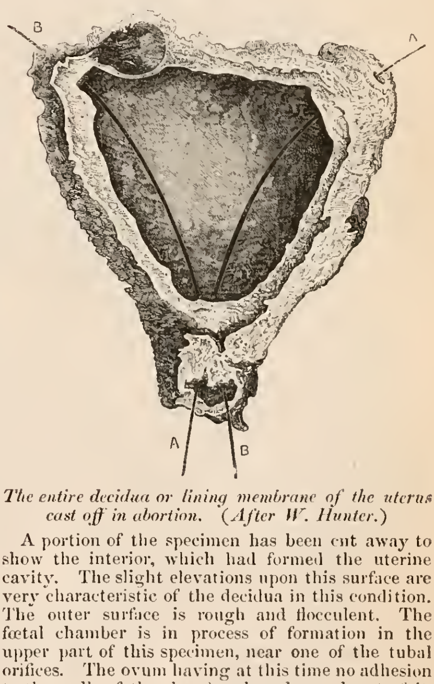
At this time all the uterine tissues have begun to expand and grow, and the uterine cavity, the walls of which were previously nearly in contact, to enlarge after the manner which in pathology constitutes eccentric hypertrophy. But, according to the foregoing description, this cavity now no longer forms one, but two compartments, the one partly inclosed within the other.

Of these two chambers, the newly formed and smaller one contains and supports the ovum, and subsequently the fœtus. It may therefore be termed the fœtal chamber; the other constitutes the original cavity of the uterus, and may be distinguished as the uterine chamber; according to the views of Breschet, it is the hydroperionic cavity. As the fœtal chamber enlarges, and the decidua reflexa becomes more expanded in consequence of the growth of the contained ovum, it gradually encroaches upon and finally obliterates the uterine chamber, which can no longer be distinguished as a separate cavity after the fifth or sixth month of gestation.

It will be necessary to examine separately the general characters of these two decidual coats. That which lines the uterine cavity may be first noticed. The parietal decidua, at the very earliest period of pregnancy in which it can be examined, forms a soft and spongy layer, 1—2‴ in thickness. That surface which looks towards the uterine cavity is elevated into numerous projections, which may be roughly compared to the cerebral convolutions, though relatively much flatter and less regular than these; between them are numerous little furrows or channels. The whole surface, both in the sulci and elevations, is covered by numerous minute perforations, corresponding with those formerly described as the orifices of the uterine glands in the unimpregnated uterus. But these orifices, from being enlarged, may now be easily distinguished by the unaided eye. They give to the surface a fine cribriform aspect. All these characters are more or less observable also in the decidua lining the uterus, in cases of extra-uterine (tubal) gestation. Along the marginal lines formed by the angles of the cavity, where the decidua is always thinnest, these apertures are large and expanded, but in the elevated spots they are often closed, apparently from lateral pressure, occasioned by the rapid growth of structure.

When early abortion takes place, the whole lining of the uterus, including the decidua reflexa, is often thrown off entire, forming a

Fig. 450.



The entire decidua or lining membrane of the uterus cast off in abortion. (After W. Hunter.)

A portion of the specimen has been cut away to show the interior, which had formed the uterine cavity. The slight elevations upon this surface are very characteristic of the decidua in this condition. The outer surface is rough and flocculent. The fœtal chamber is in process of formation in the upper part of this specimen, near one of the tubal orifices. The ovum having at this time no adhesion to the walls of the chamber, has dropped out of it. Bristles are introduced at the orifices corresponding with the Fallopian tubes, and pass out at the internal os uteri, the cervix not contributing to form the decidua.

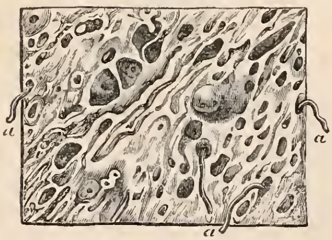
cast of the uterine cavity. If this occurs in the first fortnight of gestation, the mass retains the triangular form of the uterus. In each of the three angles is generally found an aperture corresponding with the points at which the membrane had been torn off from its continuity with the lining of the Fallopian tubes and cervix uteri.

The outer, or dorsal surface of the substance expelled, is always rugged. It exhibits numerous little papillary or club-shaped elevations, and between these much smaller cup-like or conical depressions, which are seen by transmitted light to lead, where the membrane is thinnest, directly into the apertures observable on the inner surface. At the thinnest points of all, these apertures are so wide, and the cup-like depressions so shallow, that the part has the appearance of a net, the meshes of which still consist of the enlarged orifices of the utricular glands. Hence the epithet "lace-like," often applied to the decidua in this condition.

The roughness of the dorsal surface of this, the parietal decidua, is occasioned by the membrane having been torn away from its connexion with the muscular coat of the uterus, in the act of abortion. The club-like projections are apparently the bases or blind ends of the hypertrophied utricular glands torn out entire from the substance in which they were previously embedded. When laid open, they are found to contain a small cavity. The cup-like depressions are the halves, or portions of similar, perhaps smaller glands, torn across, so as to leave other portions still attached to the uterus. The meshes are simply the orifices of such glands and of the channels leading to them.

At this and subsequent stages there may be often seen lying within and among these orifices, fine, thread-like ramified filaments, which some physiologists suppose to be utricular glands, or their epithelial lining, now becoming loosened out and falling away, — a view in which my own observations do not enable me to coincide. See *fig.* 451.

Fig. 451.

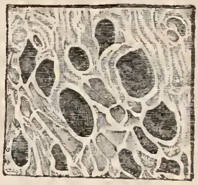


External surface of the decidua vera, from an ovum of about two months; showing the oblique channels in its substance. (*After Schrœder van der Kolk.*)

a a a, filaments supposed to be the loosened utricular glands (?)

As pregnancy advances to the third and fourth months, the uterine chamber expands, the decidua which lines it increases in thickness in parts to 3—4‴, and becomes at the same time more spongy, so that upon section it appears to be composed of flattened spaces or cells, communicating together by wide valvular orifices. These are best seen by examining under water the rough surface of an aborted ovum at that period, or the corresponding portion of the uterus from which it had been torn off. (*Fig.* 452.) These cells, or areolar spaces, continue to be seen, more or less distinctly, in the decidua throughout pregnancy, but are most conspicuous near the margins of the placenta.

Fig. 452.



Surface of the decidua vera more advanced. (*After Schrœder van der Kolk.*)

It is here represented as still attached to the walls of the uterus after the chorion, together with a layer of the decidua, have been peeled off from it. From a uterus at the sixth month of pregnancy, just beyond the margin of the placenta. The orifices and canals are much wider than in the first figure.

They are still divisions of the same ramified canals, or uterine glands, which have been described as found everywhere in the lining membrane of the uterus before impregnation, *fig.* 438., but now become so dilated and tortuous as scarcely to be recognisable as the same structures.*

In the latter months of pregnancy, the parietal decidua becomes thinner, and loses much of its spongy character, except immediately around the placenta, where this is still most distinct. It ultimately becomes blended with the outer surface of the fœtal membranes, and is partly thrown off with them in the act of birth, while a part remains, forming a honeycomb layer, attached to the uterine muscular coat.

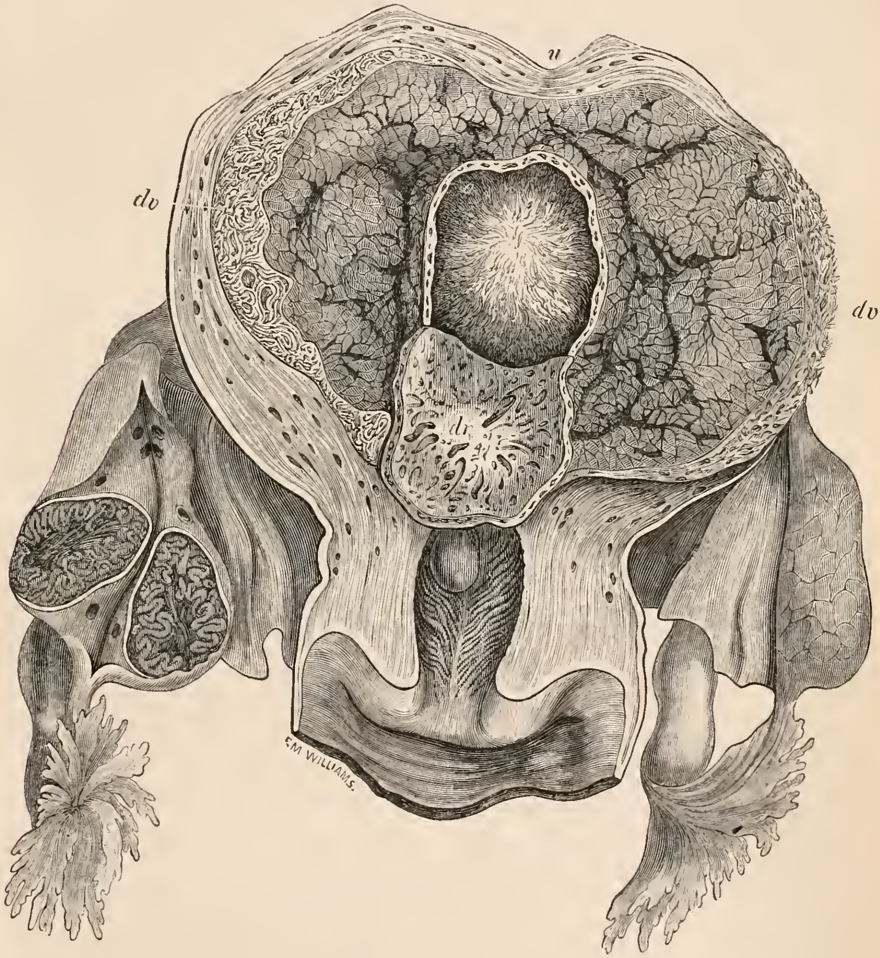
If next the growth of the *decidua reflexa*, or *decidua ovuli*, be traced, this will be found to undergo a development corresponding with that of the ovum, which it encloses and protects. The little chamber containing the ovum, which, as already stated, usually occupies a situation near one of the upper uterine angles (*fig.*450.), although it may also be found near the lower orifice (Hunter, "Gravid Uterus," *pl.* 34., *fig.* 4.), or elsewhere, appears at first like a small superadded cavity upon the outside of the larger one, or that formed by the parietal decidua. But as the development proceeds, the fœtal protrudes gradually into the uterine chamber, in the form of an incomplete sphere, whose upper pole rises free into the

* The four figures 450, 451, 452, and 453., showing the decidua or lining membrane of the uterus in different stages of development during pregnancy, should be compared with *figs.* 438, 439. and 443., which exhibit the same structure in different conditions of the unimpregnated state. These structures form a developmental series, the individual stages of which are often dislocated from their true and natural sequence by the employment of terms calculated to give an impression that the parts spoken of are different in structure and composition. "Mucous or lining membrane of the uterus," "Lymph," and "Decidua," when so employed, should be read as convertible terms representing the same part in different stages of development.

uterine cavity, but the lower forms an attached base of greater or less breadth, which is continuous in its entire circumference with the parietal decidua. The two chambers are totally distinct, and have no communication with each other. In aborted specimens, an aperture may be sometimes seen in the base or outer surface of the fœtal chamber, or that part which has been torn away from the uterine substance. In a very early specimen in my possession, and also in another which I have examined, one or more points are distinguishable also upon the upper or northern pole of the little spherical chamber, which have the appearance of apertures recently closed. Coste, in his beautiful series of illustrations*, directs attention, in several figures, to a similar spot in the same situation, having the appearance of a recently closed aperture, or umbilicus. These traces of openings in both the upper and lower poles of the sphere, are of consequence, in reference to the explanation which will be presently offered of the mode of formation of the decidua reflexa and fœtal chamber.

The outer surface of this chamber is nearly

Fig. 453.



Uterus in the first month of gestation; showing the formation of the fœtal chamber by the decidua reflexa, more advanced than in fig. 450. (*After Coste.*)

u, uterine walls laminated and traversed by numerous vessels; *d v*, decidua vera or developed lining membrane of the uterus, the uterine glands or canals being much enlarged; *d r*, decidua reflexa, in which lies *o*, the ovum, at this stage often still unattached; *c*, corpus luteum.

smooth. Upon it, however, are seen the orifices of numerous uterine glands. These are usually wanting near the centre, or umbilicus, but become more distinct towards the

* Histoire Générale et Particulière du Développement des Corps Organisés.

circumference, and are very numerous, large, and close set, in the decidual fold at the base, all round the line of apparent reflexion.

Numerous flat vessels, obviously veins, terminating in minute subdivisions, are seen ramifying over the whole surface, but becoming very scanty, or ceasing near the central point. They are continuations of similar vessels, which are still more conspicuous upon the parietal decidua. The capillaries in which these vessels terminate are exceedingly numerous, and may be sometimes seen deeply injected with blood. This is rendered the more conspicuous when the congestion is unequal, so as to form patches of a bright pink, alternating with other portions of a pale flesh colour.

The internal surface of the fœtal chamber, after the ovum has fallen out, or has been removed, presents a slightly uneven appearance, occasioned by numerous very shallow pits or depressions, occurring in close-set groups, and resembling, upon a small scale, the areolæ upon the inner surface of the heart.

When the body of the embryo begins to acquire length, the entire ovum exchanges the spherical for the slightly oval form, and to this the fœtal chamber also becomes adapted. Such is found to be the form of the fœtal chamber, sometimes in the latter half of the first, but generally during the second month, and from this period onwards the ovate figure prevails.

In the latter part of the first month, or at latest in the beginning of the second, the ovum, previously lying loose in the fœtal chamber, begins to be attached to the walls which surround it. This attachment is effected by the extremities of the villi, which from the first equally surround the chorion, everywhere becoming attached to the little pits and anfractuosities upon the inner surface of the fœtal chamber just described. In this way the embryo, surrounded by its amnion and chorion, becomes securely anchored in the midst of its little chamber, through the instrumentality of the villi, which, spreading in all directions, may be compared to the rays of the geometric spider's web.

Thus to receive, to protect, and support the ovum, and to prevent its escape from the uterus, appears to be the first object of the formation by the reflected decidua of a separate fœtal chamber (*fig.* 453.).

Ultimately, as the ovum grows, the base of its chamber expands, and here takes place a more dense and rapid growth of decidua. This is the part commonly termed the *decidua serotina*. Here the chorion villi, which now form large ramified groups, attach themselves, and from the margins of the collections of sulci just described, into which the villi penetrate, and which are now much extended, there proceed offsets or dissepiments of decidual structure. These dip down between the groups of villi sometimes as far as the surface of the chorion, and divide that which was formerly one continuous collection of ramified chorion fringes, into the separate lobes which characterise the mature placenta.

One or two points remain to be more explicitly stated. It may be asked, how does the ovum gain the interior of the fœtal chamber, or, in other words, how is the decidua reflexa formed around it? In reply to this, little beyond conjecture can be offered. Of the numerous explanations which have been attempted, few are found to meet all the peculiarities of the case. It is most probable that either the ovum becomes embedded in some of those folds of decidua which are found in it at an early period of pregnancy, and so the decidua becomes built up around it, as Sharpey and Coste suppose. Or, as it appears to me more likely, the ovum, on first reaching the uterine cavity, drops into one of the orifices leading to the utricular follicles, and in growing there draws around it the already formed, but soft and spongy decidua constituting the walls of the cavity. The chief support for such a conjecture, beyond its apparent probability, is the fact ascertained by Bischoff, who, in one case in the guinea-pig, found the ovum in precisely this situation at the bottom of a uterine follicle.*

The entrance of the ovum into the decidua being supposed, the rest of the growth of the reflexa is easily followed. The ovum now, in enlarging, raises the walls of the chamber, in which it lies, just as the skin becomes raised by the accumulating contents of a subcutaneous abscess. The process is probably in part purely mechanical, and in part in the nature of an excentric hypertrophic growth; for the actual substance of the chamber is much increased beyond the material of which it was at first composed. That some of this is borrowed from the parietal decidua, is very probable from the number of orifices of utricular glands seen upon its surface, which serve to show that the decidua reflexa is so far formed out of pre-existing structures; but much is also due to the further development of the elemental decidual tissues; and to the growth of these, the large vascular supply, which the reflexa at first receives, doubtless contributes. The little point, or umbilicus, observed sometimes at the upper pole of the fœtal chamber, may mark the spot at which, upon either of the foregoing hypotheses, the ovum first entered the decidua.

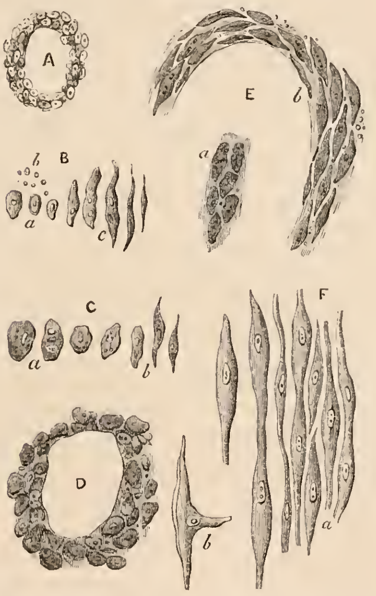
Another question which has never been satisfactorily determined, relates to the ultimate fate of the decidua reflexa. Dr. Hunter, from observing that, at the time of birth, only one layer of decidua can be found upon the secundines, supposed that, after a certain period of pregnancy, the decidua vera and reflexa, having come into contact, united to form one membrane. Doubting this explanation, I have made many observations, with a view to settle this point; and from these I

* While these sheets are passing the press, I have received the last part of Otto Funke's "Lehrbuch der Physiologie," 1857, in which the same suggestion is offered, exemplified by the same case, which, indeed, is the only one yet known.

am satisfied that no such union takes place; but that, when the decidua reflexa has fulfilled the offices already assigned to it, and has ceased to be vascular, so that no further addition of material to it can take place, it becomes, after the fifth or sixth month, so completely attenuated by distension from the growth of the ovum within, that it is reduced to a mere film, of which the only trace left at, or indeed before, birth, is a narrow frill still discoverable at the margin of the placenta between the decidua vera and the chorion. But the decidua lining the uterine walls continues vascular to the last; and this alone constitutes the membrane a part of which at birth is found adherent to the outer surface of the chorion, and which Dr. Hunter, from observing that it now consisted of only one layer, imagined was formed of the two deciduæ united together.

Histology of the decidua. — The morphological changes effected during pregnancy in the

Fig. 454.



Histology of the decidua. (*After Schrœder van der Kolk.*)

A, orifice of utricular gland of an unimpregnated adult uterus surrounded by round epithelial cells; B, cells of decidua in an ovum of about three weeks; *a*, round and oval nucleated cells; *b*, fat granulations; *c*, cells, from a deeper layer, elongated and beginning to form fibres; C, the same from an ovum of five weeks; *a*, round and oval cells, much enlarged, and containing nuclei and fat granulations from the surface; *b*, elongated cells from a deeper layer; D, orifice of a utricular gland from the same ovum, much enlarged as compared with A; E, margin of a valvular opening in a deeper layer of the decidua, from an ovum of two months; at *b*, the cells have become elongated, at *a* they are filled with fat granulations; F, long and broad cells from a decidua of nine months; *a*, the cells exhibit a nucleus, some having one and others two nucleoli; *b*, three-pointed cell.

decidua, and the chief purposes of these, having been stated, the histological peculiarities will now be briefly described. The lining membrane of the uterus, from infancy onwards, is composed, as already shown, of free elementary corpuscles or nuclei, contractile fibre cells, amorphous tissue and epithelium, together with capillary vessels, and the tortuous canals termed uterine glands. These undergo important modifications, which serve to explain the great and rapid growth of the decidua during pregnancy. According to Schrœder van der Kolk, who has traced and figured with great care the several stages of development of these elemental tissues, the cells of the decidua, surrounding an ovum of about three weeks, situated nearest the villi, have already undergone considerable enlargement. These occurred in the form of oval nucleated cells (*fig.* 454. *B a*), with fine nuclei and fat granules, *b*, intermixed; while in the layer of the decidua, still deeper, occurred longer cells, that were already beginning to form fibres.

In an ovum of five weeks, similar cells were found, in a further stage of development. In the superficial decidual layers, the oval cells, *C a*, were filled with granules, and contained a nucleus, and some a nucleolus. In the deeper layers, as before, the cells had become more elongated, *C b*. In and between all these cells were numerous minute fat granules, and among the cells lay fine nuclei. The openings of the utricular glands, *D*, which were surrounded by enlarged epithelial cells, were now considerably expanded, as compared with their usual condition previous to impregnation, *A*.

At two months, the increase in size of the oval cells, *E a*, now abundantly furnished with fat granules, was still more marked. These were developed into long cells, *b*, which were found composing those valve-like membranous septa formed now everywhere on the deeper decidual layer, as already described, *fig.* 452.

From this period onwards, the development of the cells proceeds more and more rapidly, until those in the deeper layers become transformed into fibres, which it is impossible to distinguish, under the microscope, from the peculiar contractile fibre cells of the true muscular structure.

In the ninth month are found colossal fibre cells, *F a*, which are rarely seen beyond the margin of the placenta. These were very transparent, and exhibited, some one, and some two, nucleoli. A remarkable three-pointed cell is sometimes also observed, *F b*. Fibres of fibrous tissue occur everywhere, and between them small cells and nuclei. The utricular glands have long ceased to be discernible in the advanced stages of pregnancy.

According to the observations, however, of Rolin, Robin, and Kilian, from the fourth or fifth month onwards, the decidua begins to lose the character of energetic life, which, up to that period, it had exhibited, and becomes atrophied, and less firmly adherent to the uterine walls; while, between it and the muscular parietes, there appears a new formation of decidua, at first soft and delicate, but which gradually acquires the peculiar characteristics of that membrane. This layer is not thrown off at birth, nor dispersed in the lochia, but remains attached to the inner uterine surface, and forms the foundation of the new mucous membrane, with which, after labour, the uterus is furnished. M. Robin supposes that this new soft layer is often mistaken for a product of inflammation occurring in puerperal and other uterine maladies.

e. The uterus after parturition.

Immediately after labour, the uterus, if entirely empty, occupies the whole of the pelvic cavity, together with the lower portion of the hypogastric region. The bulk of the organ varies in different individuals, and is considerably greater after twin or multiple pregnancy.

The tissues generally are of a redder colour, and softer, and more easily lacerable than in the unimpregnated condition; those of the cervix being usually more lax than those of the body, from infiltration of serum, and occasionally, in parts, of blood.

The cervical mucous membrane, which is retained*, after labour exhibits here and there sometimes slight lacerations, extending occasionally into, or through, the proper tissue of the part. In other respects, the internal aspect of the cervical canal resembles that of the same part in the last month of gestation, except that the large and voluminous plicæ (*fig.* 446.) have become folded out and flattened during the previous act of labour. Around the margin of the internal os uteri may be seen a thin ragged fringe marking the point from which the decidua, here usually much attenuated, had been torn away.

The entire uterine cavity is denuded; it presents everywhere, except at the placental space, a rough, flocculent, and sometimes honeycomb-like surface, caused by the detachment of a portion of the decidua and its discharge along with the fœtal membranes. Another portion remains covering the muscular structure of the uterus, but is in parts so thin, that the latter appears to be left nearly bare.

The surface to which the placenta had been attached forms usually one-third of the entire inner superficies of the contracted uterus. This, which is termed the placental space, is easily distinguished by its uneven, rugged, and somewhat nodulated appearance; caused chiefly by the presence of numerous large veins, whose truncated orifices obstructed by coagula here protrude slightly above the general level.

Upon section, the uterine walls exhibit everywhere the same laminated arrangement of the proper tissues, with numerous intermediately lying tortuous arteries and flattened veins and sinuses, already described as observable in the uterus during the latter periods of pregnancy (*fig.* 449.).

These flattened thin-walled veins are usually empty, or contain a few unadherent coagula. Those, however, which occupy the seat of attachment of the placenta, where they are much larger than in any other situation, are filled with dark or greyish-red clots adherent to their walls, and closing their mouths, which terminate directly upon the uterine cavity.

The peritoneal coat of the recently emptied uterus is of a pale pinkish-white colour, and presents a smooth, shining, and in parts a slightly wrinkled surface. It is thicker and less diaphanous than the same membrane before labour.

The process of involution. — No rapid or material alteration in the size or composition of the organ occurs during the first few days after labour. In the course of the first week, however, commences a series of important and interesting processes, continued during the greater portion of the two months immediately following labour, and having for their object the restoration of the uterus to a condition similar to, though not identical with, its state before impregnation. These changes consist in a gradual diminution in the weight and dimensions of the organ accompanied by a corresponding metamorphosis and ultimate reconstruction of its tissues. They together constitute the process commonly termed the involution of the uterus, which will now be examined.

Changes in dimensions and weight.—According to repeated estimates made by Heschl, the weight of the uterus, immediately after labour, ranges from 1 lb. 6—7 oz., ordinarily, to 2 lbs. 5—7 oz.; the latter being the weight after twin labour.

The dimensions depend upon the degree of contraction. Under ordinary circumstances, the entire length is 8—10 inches, and the thickness of the parietes 1 inch. These first changes in the dimensions of the organ, as compared with the state previous to labour, are effected solely by the contraction of the uterine fibre. They consist chiefly in a rearrangement of relative position in the component tissues, by which, while the entire substance of the uterus remains undiminished, its length and breadth are greatly reduced, and the thickness of the parietes correspondingly increased. In one respect, however, the entire bulk and weight are less than they were before labour, because a much smaller quantity of blood now circulates in the walls, but the solids remain unaltered.

At the end of the first week, the diminution of the organ is not very considerable. Its weight is merely reduced from 1 lb. 6—7 oz. to 1 lb. 3—4 oz. At the end of the second week, the rate of diminution is found to have been much more rapid; the organ now weighs only 10—11 oz. At the end of the fifth week, 5—6 oz.; and in the course of the second month, it is reduced to its ordinary weight of 1½ to 2½ oz.; but it never entirely regains the

* For the discussion of this question, see the works of Heschl, Robin, and Kilian, hereafter quoted.

small size and dimensions characteristic of the virgin state.

Metamorphosis and restoration of the component tissues. — The first and immediate reduction in size of the uterus, after parturition, has been just stated to depend upon mere contraction of the uterine fibre. But contraction alone will not account for those great and remarkable reductions in the dimensions of the organ which have been just described. The true explanation of these phenomena is furnished by a series of metamorphoses affecting more or less the entire uterine tissues, by which the greater portion of those structures which have been formed during pregnancy, become disintegrated and removed, while other and new tissues are developed in their place.*

In these metamorphoses, the colossal fibre cells, which form the great bulk of the newly added material, play the most important part. These have been traced, during their development in pregnancy, from the small fusiform cell of the unimpregnated uterus to the fully formed fibre of the organ at term. The growth of these proceeds *pari passu* with that of the fœtus, for whose expulsion they are destined; and this act being accomplished, their destruction and removal becomes a necessary prelude to the recomposition of the entire organ upon the same type as before impregnation. In this respect, the aggregate formation of fibre cell is comparable to the deer's horn, the placenta and other structures which, having served the purpose of their formation, and being incapable of suffering retrogression, become caducous, with this difference, however, that the one class of structure being thrown off in a mass, the act of separation is striking and obvious; while the deciduous process in the other is gradual and fragmental, and can only be discovered by the most patient and careful scrutiny.

The disintegration and removal of the uterine muscular fibre is effected, first, by the transformation of each fibre into molecular fat. This process does not commence earlier than the fourth or sixth day after labour, and not later than the eighth day. Certain differences are observable in the order of retrogression. Thus the process begins somewhat later in the inner than in the outer laminæ, while the cervix remains unchanged a few days longer than the body. In the individual fibres, the process of decay begins at many points simultaneously. The fibres lose their sinuous outline, and become paler; while within them appear yellow oil granules, commonly arranged in rows. The nucleus of the fibre is pale, but distinct, until it becomes obscured by the increase of the oil granules; while the extremities of the cells, on account of their tenuity, are the first to suffer disintegration.

Fig. 455.

Process of involution or disintegration, and renewal of the uterine fibre after parturition. (After Heschl.)

a, the old fibres filled with fat granulations 2 — 4 weeks after delivery; *b*, development of new fibres in different stages, about the fourth week.

During the second and third week, the process of disintegration continues; and it is probable that a considerable absorption of effete material now takes place, since it is not easy to explain otherwise that rapid diminution in bulk, especially in the second week, which the entire organ undergoes, as shown by the calculation of weights already given. As a result of these molecular changes, the uterus now loses its reddish colour, and becomes of a dirty yellow, and is at the same time more easily lacerable.

In the course of the fourth week, and possibly sometimes during the third, there appears, in the midst of the now degenerated fibres, the first traces of a new formation of uterine substance. These occur first in the form of cell nuclei, which are concurrently developed at several points; and gradually, while the last portions of the old muscular coat are being disintegrated and absorbed, acquire the character of the new muscular fibre cells (*fig.* 455. *b*). So that, by the end of the second month, the reconstruction of this portion of the uterine substance is often complete.

The disintegration of the remains of the decidua, and the reconstruction of the lining membrane of the uterus, which had been removed during the act of birth, is effected by a process very similar to that just described.

With regard, first, to that portion of the inner uterine superficies, which had been covered by the placenta, it is observed that this undergoes a somewhat slow retrogression. The veins, filled by thick clots in the normal state in consequence of the progressive involution of the intermediate uterine substance, occasion here a marked protrusion; so that very often, after four or six weeks, the placental space forms an elevated spot of twice

* On this subject the following may be consulted with advantage: — Dr. R. Heschl, "Untersuchungen über das Verhalten des menschlichen Uterus nach der Geburt," in the Zeitschrift der kais. kön. Gesellschaft der Aerzte zu Wien. 1852. B. ii. p. 228.; F. M. Kilian, "Die Structur des Uterus bei Thieren," *loc. cit.*; Schrœder van der Kolk, *loc. cit.*

the circumference of a dollar. Finally, however, these coagula are removed, and, together with the veins, disappear, while the place sinks to the level of the surrounding parts; and, after becoming smooth and receiving an investment of mucous membrane, is generally no longer discernible. The restoration of the placental space to its former condition does not, however, always proceed normally. Sometimes, in consequence of excessive activity in the process of reconstruction, hypertrophic growths of the new material take place; so that, several months after labour, a tumour of more or less considerable size, formed at the expense of the uterine tissues, is found to occupy the original seat of the placenta. I have satisfied myself by several microscopic examinations of the correctness of Heschl's opinion, that in this way are formed some of those anomalous-looking fleshy substances which are occasionally discharged from the uterus, and are regarded as moles.

The *histological* changes, which take place after labour in the tissues lying internally to the muscular coat, up to the complete restoration of the mucous membrane, have been examined by many observers, not always, however, with corresponding results. It appears certain that a portion at least of that layer of decidua which is still left attached to the uterine walls, is removed by fatty transformation, and that many of the products are discharged by the *lochia*. Schrœder van der Kolk has traced this process as it occurs in the nuclear cells and fibres, which form so large a portion of the decidua. Those very broad fibre cells, which are visible in it up to the ninth month of pregnancy, are no longer to be found four or five days after labour, when they appear to be transformed into long cells, through an abundant fatty transformation which progressively continues, until, by the increasing development of the oil granules and the corresponding diminution of the cells and fibres, the situation of the latter can ultimately only be discovered by the still existing longitudinal direction of the fat nuclei, while all traces of a cell wall have entirely disappeared.

Without the aid of the microscope, however, it may be seen that, a few days after labour, the entire inner surface of the uterus is covered by a more or less red soft pulpy substance, which has the same anatomical composition as the decidua. This, which is considered by some physiologists as identical with the layer of decidua already described, as formed, according to Kilian, Robin, and others, as early as the fourth or fifth month of gestation, is not discharged after labour, but becomes the seat of that reparatory process, by which the restoration of the mucous membrane upon the uterine body is effected. Between the twentieth and thirtieth day, this layer begins to resume the character of a mucous membrane. It is at first more pulpy, and softer, and thicker than mucous membrane in a normal state. The vessels become distinct in it about the third week, and sometimes still later. Previous to this, the blood appears to be contained in simple channels between the elongating cells.

The epithelium is as yet hardly formed. By scraping the inner surface of the uterus twenty days after labour, Schrœder found still only the remains of half decomposed cells. But no new cells with cilia could be yet with certainty discovered.

The utricular glands make their appearance last of all. In several cases, Heschl found them completely formed at the end of the second month; but previous to this, their development could not be traced.*

Finally, it may be said that the restoration of the mucous membrane, with all its peculiar structures, is completed about the sixtieth or seventieth day after delivery, *i. e.* by the time that the uterus is reduced to its normal bulk.

Thus it appears, that the act of involution consists in two processes, which are concurrently performed, yet with opposite purposes. For the act of reconstruction being commenced long before the retrograde metamorphosis is complete, the result of both is, that a restitution or reconstruction of certain tissues of the uterus, more or less complete, takes place.

With regard to the muscular coat, it is perhaps not any overstatement of the fact to say that each ovum is provided with its own series of fibres for the purpose of effecting its expulsion, and that these, after parturition, entirely disappear, or at least can no longer be recognised, while a new series of embryonic or undeveloped forms appears in their place. The same may also be said of the decidua, though with certain differences as to the time and mode of its destruction and renovation. Regarding the fibrous tissue of the uterus, little has been determined with accuracy; but enough has been observed to render it probable that this also, to a certain extent, becomes subject to fatty transformation. The blood-vessels appear to be likewise partly involved in a similar process, although their principal trunks probably suffer but little change beyond a material diminution of size. The peritoneum is that tissue which undergoes the least apparent alteration. It preserves, however, a thickness proportionate to the reduced bulk of the organ, and consequently it must suffer a corresponding involution.

Regarding the puerperal alterations in the nervous system of the human uterus, but little is known. Kilian†, after examining a specimen at eight, and another at twelve days after labour, as well as the uterus of many animals at different periods, arrived at no definite conclusions. He thinks it in the highest degree doubtful, that, in the puerperal state, the nerve fibres undergo the same involution process as the other tissues; viz. that the old fibres are entirely destroyed, and become replaced by a new, younger, or embryonal

* By Kilian they are said to be formed during pregnancy.

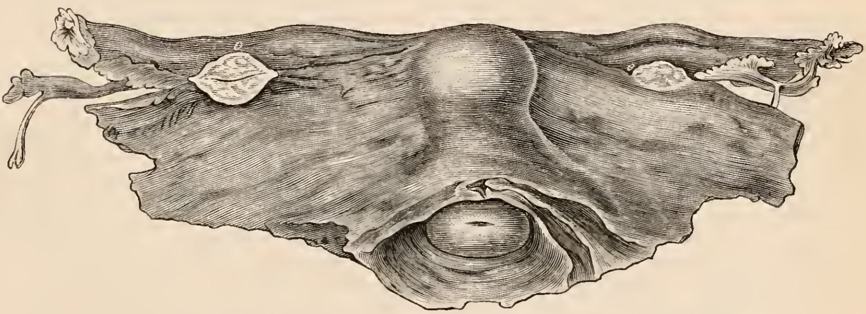
† *Loc. cit.*

form. He rather conceives that a reduction so takes place, that either the contents of the nerve fibre are partly or entirely removed by resorption, so that there remains, according to circumstances, a partly or entirely empty sheath; or that the contents of the fibre are transformed in the same manner that Günther and Schön (Henle, Allgemeine Anat. p. 771.) observed in divided nerves; viz. that the contents of the tubules become coagulated, as after death, and are then subject to resorption: the fibre appearing then to be perishing, and ribbon-like, and the contents to be disappearing. Regarding the human uterus, he thinks it in the highest degree probable, that the nerve fibre is included in the energetic resorption process that affects the puerperal uterus generally; that a reduction of the fibre follows; and that, in the next pregnancy, it again becomes developed *pari passu* with the development of the other tissues.

f. The uterus after the menstrual epoch, and in old age. — Whether the uterus has been employed, in its ultimate office, in the process of reproduction, viz. that of gestation, or whether it has proceeded only so far towards this as to have been limited to the repetition, in unvarying succession, of that preparatory stage which is expressed by the minor function of menstruation, in either case the period equally arrives at which the activity of the organ passes away. Ova are no longer discharged from the ovaries. These cease to be creative or developing organs; and with this cessation of the proper function of the ovary, there comes also a corresponding diminution, and finally a termination of the correlative offices of the uterus.

It is now interesting to observe how the uterus gradually resumes some of the peculiar features which it exhibited at an earlier period of life. It may be said to fall back again into its infantine condition. For with the shrivelling of the ovaries, and their reduction to a size as small sometimes as that of a child of two or three years, (*fig.* 456.) the uterus also gradually shrinks, not in all its parts, but principally in the body, or that portion which is chiefly employed in the processes of menstruation and gestation. This part becomes atrophied more than the rest; its walls become thinner, partly from diminished circulation in them, and partly from atrophy of the component tissues, which appear pale and nearly bloodless. Thus it happens that, in advanced life, the walls of the uterine body, no longer possessing that fulness which at an earlier period caused them to encroach upon the cavity, and to exhibit that incurvation of the sides and fundus which has been described as characteristic of the mature organ, again return to the straight and more attenuated condition which they had in early life. We may often observe, therefore, in the uterus of aged persons, a nearer approach to the form of the equilateral triangle, caused by the shortening of the body and the straightening of its walls, than is seen in the uterine cavity of mid-life; and it is this return to the form of the fœtal cavity, together with the now preponderating size of the cervix, which remains nearly unchanged, that gives to the aged uterus its greatest similitude to that of infancy or early youth.

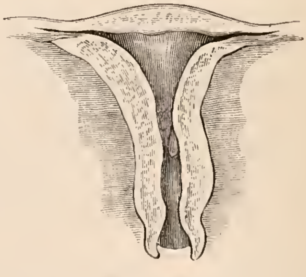
Fig. 456.



The uterus in old age; showing a return to the infantine proportions between the body and cervix.

o, the shrivelled ovaries.
This figure exhibits the parts of half the natural size. (*Ad Nat.*)

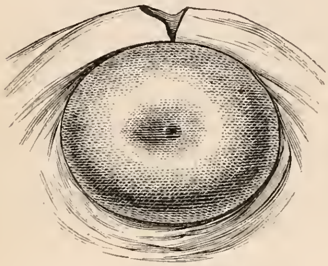
Fig. 457.



Thinning of the uterine walls in old age, and return to the triangular form of the cavity characteristic of the infantine (fig. 442.) and undeveloped uterus (fig. 465). (Ad Nat. Half the natural size.)

But these changes are not limited to the body of the uterus. The external uterine orifice being now no longer required to serve as a conduit for fluids to or from the uterus, or for the passage of more solid contents, becomes reduced in diameter, and may sometimes be observed to possess an aperture that would hardly admit the head of a moderate sized probe.

Fig. 458.



Os uteri in old age. (*Ad Nat.*)

Functions of the Uterus.

The uterus, in common with the rest of the generative organs, being concerned only in the reproduction of the species, its offices are limited to that period in which the animal functions are maintained in their highest state of efficiency. The growth of the body is nearly or quite completed before the sexual offices commence, and the power of reproduction continues as long as the frame is maintained in full vigour; but when the age arrives at which the animal functions generally begin to decline, their decay is anticipated by the total cessation of the power of procreation in the female. The period, therefore, is limited, yet not brief, during which the functions of the uterus can be exercised, and on either side of this epoch the organ remains passive, except under abnormal states.

The chief functions of the uterus are those which relate to — 1. Menstruation; 2. Insemination; 3. Gestation; 4. Parturition.

The office of the uterus in menstruation. — Although the uterus is the efficient instrument in the performance of menstruation, yet the power of initiating and regulating this function resides in the ovaries, which exert a powerful reflex influence, not only upon the uterus, but also upon the entire organism. Without the ovaries, menstruation has never been known to occur. Their artificial removal is followed by a permanent cessation of the catamenial flow, although the uterus may be left uninjured; while the congenital absence of both ovaries is always accompanied by an enduring amenorrhœa.

The external sign or evidence of menstruation consists in the occurrence of a sanguineous discharge, which escapes from the vaginal orifice of women in health, periodically, except during pregnancy and lactation. This discharge first appears usually between the fourteenth and sixteenth years, and continues to be repeated at intervals of a lunar month for an average period of thirty years. The time, however, of the commencement, as well as of the decline, of menstruation is very variable, and may be either much accelerated or retarded, according to individual peculiarities.*

Periods of duration and recurrence. — The catamenial period and interval together occupy a space of one lunar month. And in some women this function is performed with such regularity that the day, and very nearly the hour, of its expected return may be predicted. The natural duration of the flow varies from three to five or even seven days. An interval then occurs during which the flow entirely ceases. This occupies from twenty-one to twenty-five days; and it is during the first half of this interval that conception most commonly takes place.

It cannot, however, be asserted that this degree of regularity is observed even in the majority of women. Frequently the period of regular return is anticipated by one or more days; or, on the other hand, it may be retarded, without the occurrence of any concomitant disturbance of other functions, such as would justify the regarding of these examples as abnormal. But whatever may be the amount of variation — dependent in most cases upon idiosyncrasy, — still a law of periodicity is observed which, in all ages and countries, has been recognised, and more or less distinctly expressed by such terms as catamenia, menses, courses, periods, règles, mois, monatlicher Fluss, and the like.

No catamenial discharge takes place normally during pregnancy or lactation. Exceptions to both these rules, however, occur, and instances of the latter are sufficiently common. But with regard to the former, it is probable that many at least of the recorded cases of menstruation during pregnancy have been cases in which the placenta was implanted low down, or even over the os, under which circumstances it is well known that slight flooding will occasionally commence at an early period of gestation, and observe a certain rough periodicity. Upon *anatomical* grounds, a catamenial flux during pregnancy can only be supposed possible where the condition of the uterus is such as to admit of the discharge taking place from the vaginal portion of the cervix; an occurrence which is shown by Mr. Whitehead to have obtained in all the instances of supposed menstruation during pregnancy which he had investigated. For "on examining these cases with the speculum

* For much valuable statistical information relating to the periods of invasion and decline of the catamenia, and in refutation of the popular belief that these periods are greatly influenced by climate, &c., see Robertson's Essays and Notes on the Physiology and Diseases of Women; also, on the subject of menstruation generally, Whitehead, the Causes and Treatment of Abortion and Sterility; A. Brierre de Boismont, De la Menstruation, 1842; Raciborski, De la Puberté, 1844.

during the existence of the menstrual phenomena, the blood was invariably found issuing from diseased surfaces situated upon or about the labia uteri, none escaping from the interior of the organ." *

But in any case there is wanting a sufficient series of observations, taking cognisance of the exact duration and times of recurrence of such discharges, and comparing these with the normal periods and intervals of menstruation, to warrant an unhesitating belief in the occurrence of a true catamenial flow as a possible phenomenon during gestation.

Quantity. — The quantity of the menstrual fluid which escapes at each period has been so variously estimated at different times and by different observers, as to render it obvious that the calculations could not have proceeded upon any common data. Thus Hippocrates, and afterwards Galen who quotes him, states the quantity as two Attic hemina, equal to about eighteen ounces. In recent times it has been estimated by Magendie at several pounds, and Haller gives the average amount as varying from six to twelve ounces. But all these estimates are too high. Dehaen, who employed an ingenious method of measurement, calculated that some women lost three, others five ounces, and very few half a pound ; but that it was exceedingly rare for a woman who had no malady to lose as much as ten ounces.† Probably the only proceeding by which any definite result can be obtained, is that of observing the rate of escape of the discharge from the uterine orifice. According to the observations of Mr. Whitehead, this is generally so slow that no more than from ten to twelve grains could be procured during the time that the patient was able to endure the irksomeness of the proceeding. From these, and similar observations of my own, as well as from other estimates, I conclude that two to three ounces is probably the full extent of the natural flow, and that a discharge amounting to six or more ounces in the aggregate will generally produce for the time sensible effects upon the constitution, such as general pallor, and some feebleness of the muscular system.

Nature of the catamenial discharge. — There is no foundation for the belief once so prevalent, and even partially still retained, that the menstrual fluid contains materials of a noxious or poisonous nature, nor yet that it serves as a vehicle for the depuration of the blood of the female. The occasional fœtid odour of the discharge, and sometimes also of the breath of women during menstruation, arises from the decomposition of the fluid, as it slowly collects in the vagina, and doubtless also from its partial resorption into the system, producing in such cases a heavy or fœtid odour of the breath, the cause of which was pointed out more than two centuries ago by De Graaf.‡ The menstrual fluid has always, even in health, a peculiar and somewhat heavy odour which

* Whitehead, loc. cit. p. 24.
† Brierre de Boismont, op. cit. p. 68.
‡ De Mul. Organ. Lug. Bat. 1672, p. 134.

is as characteristic of it, as is the *gravis odor puerperii* of the lochial and other discharges in childbed.* But these circumstances afford no evidence that the excretion is, when first formed, necessarily unhealthy.

The menstrual fluid, when first formed, appears to consist almost entirely of pure blood ; but, in its course through the vagina, it receives in addition the secretions of that canal, whereby both its physical condition and chemical constitution are materially altered. Hence the differences of opinion which have so long prevailed regarding the real nature of this fluid, and the extent to which it differs from pure blood. These differences have been maintained chiefly by the well-known fact that menstrual blood seldom coagulates, and also by the difficulty of discovering fibrine in it. But a solution of this difficulty is found in the fact that the mucus of the vagina has always an acid reaction, and that in this acid the fibrine of the blood is so readily dissolved, that not only is its coagulation prevented, but chemical analysis fails usually to reproduce more than a trace of it.

The menstrual fluid, therefore, as escaping from the vaginal orifice, and that collected from the os uteri, are essentially two different products, and this distinction should be observed in all examinations having reference to its chemical or physical composition. But it would be perhaps arbitrary to designate either of these alone the menstrual fluid. Probably this term is most suitable to the first. Both the vagina and uterus are concerned in the production of this fluid in the form in which it is most familiarly known, and in this form it may first be examined, the pure and unmixed product of the uterus being reserved for subsequent consideration.

Composition of menstrual fluid according to M. Denis.

Water	82·50
Fibrine	0·05
Hematosine	6·34
Mucus	4·53
Albumen	4·83
Oxide of iron	0·05
Osmazome and cruorine, of each	0·11
Salts and fatty matter	1·59

Microscopic examination. — The menstrual flux exhibits three periods or stages ; viz. the periods of invasion, stasis, and decline. In the first the discharge is of a paler colour, and sometimes consists mainly or entirely of mucus — *menstrua alba.* But this stage is not always observed, the discharge often commencing at once of the deep red colour characteristic of the middle stage. This continues during the greater part of the period, and is succeeded by the third stage or that of

* Doubtless this led Pliny to draw up that dire catalogue of evils, in which he informs us, that the presence of a menstruating woman turns wine sour ; causes trees to shed their fruit, parches up their young shoots, and makes them for ever barren ; dims the splendour of mirrors and the polish of ivory ; turns the edge of sharpest iron ; converts brass to rust ; and is a cause of canine rabies.—C. Plinii, Nat. Hist. liber vii. § xiii. ed. Cuvier, 8vo. vol. i. Paris, 1827.

decline, when the discharge loses its deep red colour and assumes the hue of water in which raw flesh has been washed. This is very commonly the condition of the discharge during the last day or two of each period, especially in those women in whom the flow is of long continuance.

M. Pouchet* has examined with great care the menstrual discharge at each of these periods. The following are the results of his observations: 1*st invasion.* A very few blood globules mixed with mucus may be observed, together with mucous-corpuscles and scales of epithelium, mostly entire, floating in an abundance of limpid fluid. Almost all the mucous-corpuscles contain smaller globules or granules which form in them a central nucleus. 2. *Stasis.* Menstruation having reached its apogée, the blood-globules are much more numerous than at the onset. The plates of epithelium usually remain entire. 3. *Decline.* The fluid contains the same substances, and presents nearly the same appearances as at the time of commencement of the flow.

These observations agree generally with my own, and also with those of Donné, who found the menstrual fluid to consist of, 1. Ordinary blood-globules of the proper character, and in great abundance. 2. Mucus from the vagina mixed with epithelial scales. 3. Mucous-corpuscles from the cervix uteri.

The unmixed menstrual fluid.—But in order to determine the nature of the menstrual fluid as it issues from the uterine orifice, unmixed with the secretions of the vagina, it must be collected by a speculum accurately fitting the uterine neck. The fluid so obtained possesses properties very different from those of the flux already described. Its sensible characters, as observed in more than a dozen specimens, are well described by Mr. Whitehead. Thus procured, the fluid is never so dark in colour as ordinary menstrual blood, so called, nor so fluid always as that of the arteries. Its colour varies slightly, but whatever is its tint, this is not subsequently affected by intermixture with the vaginal mucus. It appears usually rather more viscid than systemic blood, probably on account of its slow exudation. When thus collected it invariably coagulates, the separation into clot and serum being complete in three or four minutes. It sometimes passes off in a continued stream as pure blood, but more often as a thin coloured serum mixed with small flattened clots, the size of orange seeds, which, becoming broken down and, as it were, dissolved in the vaginal mucus, appear at the external orifice in the usual uncoagulable fluid form. It is invariably alkaline.

In menorrhagia the discharge is as fluid as arterial blood, and not being delayed on account of the greater rapidity of escape, it trickles in drops along the tube.

On account of the great difficulty which is experienced in obtaining the pure fluid from the uterus in quantities sufficient for chemical analysis, the following results by Bouchardat are the more valuable. The woman, a multipara, was thirty-five years of age. To explain the large proportion of water Bouchardat states that she had subsisted chiefly on a vegetable and milk diet.

Bouchardat's analysis of pure menstrual blood.

Water - - - - -	90·08
Solid matter - - - -	6·92
The solids were composed of—	
Fibrine, albumen, colouring matter	75·27
Extractive matter - - -	0·42
Fatty matter - - - -	2·21
Salts - - - - -	5·31
Mucus - - - - -	16·79
	100·00

It will be observed that the proportion of fibrine is here much larger than in the former example. But chemical analysis is not needed to show that this element of the blood constitutes a part of the fluid exuded from the uterus. For in women who have died menstruating fibrinous clots have been found in the uterine cavity; coagula have also just been described as forming at the os uteri and mixing with the fluid collected by the speculum, and it cannot have escaped observation that clots sometimes form about the vulva, at times of menstruation, especially when the discharge is freer than usual.

But the notion that the menstrual discharge differs from ordinary blood "in containing only a very small quantity of fibrine, or none at all,"* which view has gained general currency of late, and in support of which the investigations of Brande or Lavagna are usually quoted, appears to be altogether a modern one. For the older writers considered the menstrual discharge as identical with blood. Hippocrates says in reference to it, "procedit autem sanguis velut à victimâ, et cito coagulatur, si sana fuerit mulier." Mauriceau† says that menstrual blood does not ordinarily differ in any way from that which remains in the woman's body. So also Haller and Hunter, both of whom regarded menstruation as a natural evacuation of blood.

The results of these careful investigations therefore warrant the conclusion that the menstrual fluid, at the moment of its effusion, consists of pure blood, mixed only with the small quantity of mucus and epithelium which it receives in passing through the body and neck of the uterus, and that at this point it always has an alkaline reaction. But that in the course of its passage through the vagina the original fluid becomes mixed with the mucus of that canal, which there exists in increased quantities, and that in the acid of that mucus the fibrinous portion is so far dissolved as to render the detection, by chemical means, of fibrine, as a constituent of the secretion, difficult or impossible. So much, however, of fibrine as belongs to the blood-corpuscles must always be present, for these bodies exist in

* Théorie Positive, Atlas, plate xii.

* Müller's Physiology by Baly, p. 1481.

† Traité des Mal. des Fem. Gross. p. 45. 3rd ed. 1681.

large quantities in every instance of a healthy menstrual flux.

Source of the menstrual fluid. — The vagina, the os and cervix, and the body of the uterus, have been severally regarded as the parts which furnish the menstrual flux. And so far as the mucous element is concerned it is probable that all these surfaces contribute a certain proportion; but that the blood in normal menstruation is derived mainly from the lining membrane of the body of the uterus, is placed almost beyond doubt by the following considerations: —

1. In the uterus of one who has died whilst menstruating, a remarkable difference is usually perceptible in the condition of the mucous membrane lining the cavity of the body and cervix respectively. That of the body is highly injected, of a deep red colour, the vessels distinct, and the capillaries numerous. That of the cervix exhibits a condition the opposite of this. It is pale, uninjected, and free from all appearance of distended vessels.

2. If such a uterus be injected, the same conditions are observed in a more marked degree. All the capillaries on the mucous membrane of the body are filled, but comparatively few of the cervix; an abrupt line of demarcation occurring sometimes at the internal os uteri.

3. If gentle pressure be employed, as by taking the uterus in the palm of the hand, and slightly approximating the two sides, blood is perceived to flow up from the little pores or orifices of the utricular glands, which are everywhere perceptible, upon the surface of the mucous membrane, until this collects in the cavity in a quantity sufficient to cover the surface.

4. If the same experiment be made under water, in a dish or shallow basin, with the aid of very gentle pressure on the sides of the uterus, such as could not apparently cause any rupture of uterine vessels, the little streamlets of blood are seen welling up from each pore, and mingling with the water. In neither of these cases is the blood seen to proceed from any part of the cervix, but only from the lining membrane of the uterine cavity.

5. The blood, in ordinary menstruation, is seen to flow from the os uteri into the speculum, but is never observed to proceed from the lips of the cervix, except the latter be in an abnormal state.*

6. The cavity of the uterus, after death during menstruation, has been frequently found to contain blood or a coagulum.

From these observations it may be concluded, that in normal menstruation the blood is furnished by the walls of the uterine cavity. Whether the lining membrane of the oviducts also contributes any portion of the fluid is not certainly known. But I have had reason to think this very probable, from observing that, in cases of death during menstruation, the tubes as well as the uterus contained blood, which may in some cases, however, have entered them by regurgitation from the latter. (See also p. 618.)

By what means does the blood escape from the uterine vessels in healthy menstruation? — The investigation of this question is attended by great difficulties, and data sufficient even for its approximate determination are yet wanting.

The explanations which have been offered are chiefly the following: —

(*a.*) The blood is supposed to escape in the form of a secretion.

So long as it was maintained that the menstrual fluid differed essentially from pure blood, the view that it was eliminated from the general circulating current by a process analogous to that which obtains in true secreting glands received ready acceptance, and the menstrual fluid was, in accordance with such views, denominated a secretion. But since it is now known with tolerable accuracy to what portion alone of the menstrual fluid the term secretion can, with any degree of truth, be applied, it seems useless further to argue the question of secretion or non-secretion, in reference to the main ingredient of this fluid, which has already been shown to be pure blood, unaltered in its physical and chemical constituents, until after it has become mixed with other and adventitious matters.

(*b.*) The blood is supposed to escape by transudation through the capillaries of the uterine mucous membrane.

This view, which is proposed by Coste * and others, need not be considered specially with reference to the uterus. Those who think that the blood-corpuscles, which microscopic examination proves to be abundantly present in the menstrual fluid, can pass by transudation, unaltered and entire, through the walls of capillary or other vessels without rupture of their coats, will find no difficulty in applying this explanation to the production of a like phenomenon, as it may be supposed to occur in the uterus.

(*c.*) The blood is supposed to escape through lacerated capillary vessels.

Many observed facts give to this view a certain amount of probability. Thus, in an injected uterus the capillary vessels, which form so fine a network upon its inner surface (*fig.* 439.), may be occasionally observed denuded, and hanging forth in detached loops. In such a condition I have found the vessels when death has occurred during menstruation.† Unless this is a post-mortem change, which is improbable, it may be assumed that this laying bare of the capillaries is the consequence of a vital action, whereby a portion of the epithelial and mucous surfaces are broken

* Whitehead, loc. cit. p. 24.

* Histoire du Développement, tom. prem., 1 fasc. p. 209. 1847.

† I am not prepared to assert that this condition is always present during menstruation, or that it is limited to such periods. A larger number of examples than those in which I have observed this feature would be necessary to establish such a fact; and the whole subject requires a closer examination than has yet been given to it.

down, and subsequently discharged, along with the menstrual fluid. According to the observations of Pouchet *, such an exfoliation of uterine epithelium takes place monthly in women and the mammalia generally. Pouchet, indeed, maintains that not only is there a monthly desquamation from the uterus, but that this extends to the separation and expulsion of a deciduous membrane on each occasion, and that this expulsion, which takes place in the form of the broken down elements of the deciduous lining of the uterus, constitutes the process described by him under the title of intermenstruation. Such an exfoliation, if it extended only to the epithelial cells surrounding the uterine capillaries, would simply leave them bare, but if proceeding to the extent of removing the whole deciduous uterine lining, would of necessity carry off with it the whole capillary network of vessels, (see *fig.* 539.) lying upon the face of this membrane, and consequently would leave a surface of torn capillaries, from which the hæmorrhage might occur †, and this in fact takes place in cases when dysmenorrhœal membranes are discharged (*fig.* 443.).

(*d.*) The blood is supposed to escape by permanent vascular orifices.

In the present state of our knowledge, the evidence in support of this view is not more conclusive than that upon which the preceding hypothesis is built: yet many circumstances lend colour to it. The question of a termination of the uterine vessels by open orifices has been occasionally, though obscurely, touched upon by different authors. Thus, Madame Boivin ‡, a most careful observer, after speaking of the "perspiratory orifices of extreme minuteness," visible upon the inner uterine surface, evidently meaning the orifices of the now well-known uterine glands, describes the manner in which the blood may be made, by pressure, to appear in droplets upon the inner surface of the uterus when death has occurred during menstruation; and, without giving a personal opinion, she elsewhere quotes the then prevailing views, that the blood is furnished by the exhalent extremities of arteries terminating upon the inner surface of the uterus. Dr. Sharpey § endeavoured, by various expedients, to determine what is the precise relation of the blood-vessels to these orifices in the decidua a little more advanced *, as, for example, in early pregnancy; but after expressing his conviction upon the subject, the precise anatomical connection between the two is left undetermined. Ordinarily, in injecting the uterus with fine coloured fluids, I have observed the cavity to become filled, the injection apparently escaping by the glandular orifices, which also themselves may be seen filled with injection. In some specimens a capillary branch may be observed passing to and stopping short at one of these canals or orifices, and having much the appearance of an open vessel. Without personally expressing an opinion upon this point until I have carried further some experiments now in progress, I may observe, that the idea of a permanently open termination of vessels here need not be set aside upon the objection that such an arrangement would produce a constant bleeding, because the vessels supplying the blood must first pass through a dense muscular tissue, amply sufficient to control or arrest bleeding, as indeed it does effectually after labour, when much larger mouths are laid open, and also occasionally when menstruation is suddenly arrested by powerful mental impressions, acting apparently upon the muscular fibre of the uterus; while many positive facts might be adduced in support of such a view, such as the frequent bleedings of uterine polypi, which are always invested by mucous membrane, the ready passage of fluids through the surface of the latter when their main vessels are injected, and the like.

What is the purpose of menstruation?—To this question no reply will be satisfactory which does not include the consideration of many other circumstances besides the mere escape of blood. Menstruation has evidently a much deeper signification than is declared simply by the flux, which is probably not the most important part of the function, although it constitutes the external sign or evidence of it.

Amid all the crude hypotheses of former times, such as that menstruation is due to fermentation, lunar influence, and the like, some of the older writers appear nevertheless to have had a dim perception of the truth when, under the form of an elegant type, they shadowed forth that which appears to be the real purpose of the menstrual act. The French term, "fleurs," and the English, "flowers," are now fallen into disuse; but they were employed in earlier times as designations of menstruation, for the purpose of suggesting that, after the example of trees, which do not bear unless the fruit is preceded by the blossom, so a woman does not become pregnant until she also has had her flowers.†

Menstruation is not established until the ovaries have reached a certain stage of development, and the maturation and discharge

* Théorie Positive, Huitième Loi.

† Pouchet, who does not enter upon the question of the effect which such a monthly denudation of the inner surface of the uterus would have upon its capillary vessels, nor, indeed, at all upon the consideration of the precise mode in which the menstrual fluid escapes, makes this supposed exfoliation and expulsion of the menstrual decidua occur at the periods intermediate between those of the menstrual flux. Thus the idea of a separative process, which might have been made comparable with that occurring in labour, when the entire ovum is thrown off and a bleeding surface is left, from which the lochial discharge takes place, loses its significance from the circumstance that this phenomenon is said to happen at periods when there is no bleeding.

‡ Mém. de l'Art des Accouch., quarto ed. p. 61. *et seq.*

§ Müller's Physiology by Baly, p. 1579.

* It must be observed that throughout this article the terms "decidua" and "mucous or lining membrane of the uterus" are employed as strictly synonymous.

† Mauriceau, Malad. des Femmes grosses. 1681.

of ova has commenced.* It continues to be performed as long as the process of ovulation is continued; but when the latter ceases, and the ovaries have become shrunken, their tissues attenuated and wasted, and Graafian follicles can be no longer distinguished, menstruation ceases to be performed.

These facts show that menstruation and ovulation proceed *pari passu;* but they do not alone prove that the one function is dependent upon the other.

If, however, both ovaries are congenitally deficient, no attempt at menstruation is ever observed; while, on the other hand, in cases where the ovaries are present but the uterus is deficient, puberty becomes established in due course, and then a regularly recurring menstrual molimen may be observed, although for the want of the uterus this function cannot be carried out. See note §.

Or if, under ordinary circumstances, after the regular establishment of menstruation, both ovaries become extensively diseased, or both are removed by operation†, menstruation is from that moment permanently suspended.

Hence it appears that the presence of the ovary in a healthy state is essential to menstruation.

But something more also is needed; for the ovaries may be present and healthy, yet if they cease for a time to mature or emit ova, as for example during pregnancy and lactation, when they are passive‡, then, so long as those processes endure, menstruation is also commonly suspended, but returns after the completion of one or both of them.

A series of facts so consistent appears to admit of but one interpretation: namely, that a menstruating condition of the uterus bears a direct relation to the active operations of the ovaries, and that this function is only performed under circumstances which render pregnancy possible so far as the ovaries are concerned; but if the conditions are such that impregnation cannot take place, then the uterus, although it may be healthy, does not menstruate.

But, in addition to this general relationship between menstruation and ovulation, it is necessary to determine further if any direct correspondence exists between each separate act of menstruation and the maturation or discharge of one or more ova from the ovary, so that these two acts shall be coincidentally performed.

The following evidence supports this view.

The ovaries at the menstrual periods are not unfrequently the seat of pain and tenderness, indicating some unusual activity of this part. This is most remarkable in the rare case of hernia of the ovary.§

In women who have died during a menstrual period the ovaries have been frequently observed to present unmistakable signs of the recent rupture of one or more Graafian follicles. Some examples of this fact have been already given. In one case the ovum itself was found in the Fallopian tube (p. 567.).*

Conception is supposed to take place most frequently within a few days after a menstrual period, and therefore during the time which an ovum, if it were emitted from the ovary during menstruation, would occupy in passing down the Fallopian tube and perhaps in arriving at the uterus.

Menstruation corresponds in many particulars with the œstrus, or rut, in the mammalia, and in them it is only during the œstrus that ova are emitted from the ovaries, and that conception can take place.

The foregoing facts constitute evidence bearing upon two distinct points. The first series proving that a menstruating condition of the uterus is maintained only so long as the ovaries continue in the active performance of their function of preparing and ripening ova. The second series affording a certain amount of presumptive evidence, that each separate act of menstruation is connected with or is dependent upon a corresponding act of maturation, and perhaps of spontaneous emission of one or more ova from the ovaries.

The accuracy of the first conclusion will probably not be questioned; but if the second point is to be regarded, as at present, more than an hypothesis having many facts and probabilities for its support; if, as M. Pouchet believes, we are justified in considering as established laws of generation that in man ova are emitted from the ovary at fixed epochs and at no other times, and that these occa-

* The views of Dr. Ritchie in dissent from this statement have been already noticed, p 572.

† See Mr. Pott's case, p. 573.

‡ Négrier's, loc. cit.

§ In a case of this kind recorded by Dr. Oldham (Proceedings of the Roy. Soc. vol. viii. p. 377.), both ovaries had descended through the inguinal canals, and were permanently lodged in the upper part of the external labia. At intervals of about three weeks one or both ovaries were observed to become painful and tumid, the swelling augmented for four days, remained stationary for three days, and then gradually declined; the whole process occupying generally from ten to twelve days. It happened, unfortunately, that in this case the uterus and vagina were deficient, so that menstruation could not take place; but the case in one respect is the more interesting on that account, for notwithstanding the absence of the uterus, all the external signs of puberty were present, and the evidence of a periodical activity and excitement of the ovaries, and of a menstrual molimen affecting the organs which were not malformed, were here unmistakable. These circumstances forcibly call to mind the painful condition of the ovaries which, in a similar case, induced Mr. Pott to extirpate those organs.

* Upon the connection between the discharge of ova from the ovaries, and the phenomena of heat and menstruation, the following should be consulted, viz.:—*E. Home,* Lectures on Comparative Anatomy, vol. iv., and Phil. Trans. 1817 and 1819; *Power,* Essays on the Female Economy, 1821; *R. Lee,* Cyclopædia of Practical Medicine, art. Ovary, 1834; *Gendrin,* Traité Philosophique de Médecine Pratique, t. i. 1839; *W. Jones,* Practical Observations on Diseases of Women, 1839; *Paterson,* Edinb. Med. and Surg. Journ. vol. liii; *Girdwood,* Lancet, 1842–43; in addition to the works of *Bischoff, Raciborski, Négrier, Coste,* and *Pouchet,* already quoted under the title OVARY, p. 568., where will be found a full account of the process of ovulation.

sions, which furnish the sole opportunities for impregnation, bear the same constant relation to menstruation that the acts of ovulation and the times of conception in the mammalia bear to the œstrus, it becomes necessary to examine more closely the grounds of this belief; and for this purpose the circumstances as yet ascertained regarding the times of conception in women, the condition of their ovaries, not only during menstruation but in the intervals also, and the actual relation which the œstrus, or period of conception in mammals, bears to menstruation, may be briefly passed in review.

The precise period at which conception in the human subject occurs in most cases cannot, for obvious reasons, be determined, but whenever conception can be traced to a single opportunity, the process of impregnation, or the fertilisation of the ovum by contact with the spermatozoa, may be assumed to take place within a few hours after the act of insemination; for the spermatic fluid rapidly traverses the generative canal, while here spermatozoa cease to have motion within thirty hours at latest from the time of emission.

From various methods of computation it is supposed that in a large majority of cases conception occurs during the first half of a menstrual interval, and most commonly during the first week. In sixteen instances noted by Raciborski conception occurred as late as the tenth day after menstruation in only one case.*

The number of instances in which conception can be ascertained, or may be fairly assumed, to have taken place in the latter half of a menstrual interval is comparatively small. Nevertheless impregnation may unquestionably occur during this time, and even within a day or two of the next menstrual flow, which is then usually diminished in duration and quantity, or is reduced to a mere show.

Now if we endeavour to explain these facts, relating to the times of conception, by the aid of an ovular theory of menstruation, the question may be brought within very narrow limits. One of two postulates may be assumed. An ovum emitted at or soon after a menstrual period either remains susceptible of impregnation through the whole of the succeeding interval, or it loses that susceptibility, and perhaps perishes before the recurrence of the next menstrual flow.

The first hypothesis would sufficiently account for impregnation taking place at any part of a menstrual interval; but it has little or no evidence for its support. Nothing, indeed, is known regarding the length of time during which the human ovum remains susceptible of impregnation after it has escaped from the ovary. The period of susceptibility in the mammalia generally is variable. In the bitch, as already stated (p. 606.), the ovum, after quitting the ovary, is supposed to remain in the tube during six or eight days. Its passage is probably quite completed in ten days. In the guinea-pig the period is much shorter, as the ovum enters the uterus at the end of the third day. In the rabbit also the period does not extend beyond the beginning of the fourth day. But by the time that the ovum reaches the uterus, or sometimes even the lower end of the oviduct, in most of the mammalia yet observed, the œstrus is past, and with it also the opportunity for impregnation. The evidence therefore obtainable from the mammalia fails to support the conjecture, that in man an ovum detached during menstruation can remain susceptible of impregnation through the whole of a menstrual interval, consisting of twenty-three or more days, although the period of this susceptibility *may* be longer in man than in the other examples cited.

But if this first hypothesis fails, the second appears inevitable, viz., that an ovum emitted during menstruation loses its susceptibility of impregnation before the termination of the succeeding menstrual interval. M. Pouchet supposes, that in the human subject the duration of this susceptibility does not exceed fourteen days. Consequently if, according to the strict formula of the latter physiologist, ova are emitted only at or shortly after the menstrual periods, there must remain a portion of each menstrual interval, during which every woman is physically incapable of conception. And this alternative M. Pouchet* does not hesitate to adopt.

But since this conclusion is incompatible with the facts already stated regarding the occasional, though probably rare occurrence of conception during the latter portion of a menstrual interval, and especially towards its conclusion, M. Coste, who shares with many others a belief in these facts, has proposed an explanation which constitutes a very considerable modification of the ovular theory of menstruation. To account for impregnation at a later period than usual of a menstrual interval, M. Coste supposes that a ripe or distended Graafian follicle, having failed in reaching the point of rupture, may remain stationary, as it sometimes does in mammals †, and that the influence of the male is sufficient to determine the dehiscence of a follicle in such a state. And in order to anticipate the obvious objection, that if the emission of an ovum from the ovary is the cause or occasion of menstrua-

* These and similar facts have been commonly regarded as showing a greater *aptitude* for conception shortly after menstruation; but the influence of mere *opportunity* has not perhaps been sufficiently considered; for if, as in the case of the Jews under the strict requirements of the Levitical law, the whole of the first week, or that period which is commonly regarded as most favourable to conception, be withdrawn from the opportunities for impregnation, no diminution whatever of prolific power results.

* Théorie Positive. — M. Pouchet believes that a slender decidua is always formed at the decline of each menstruation, which, together with the ovum, whenever the latter is not impregnated, is cast off from the uterus between the tenth and fourteenth day, and that after this event every woman remains incapable of conception until the next menstrual period, when the detachment of another ovum from the ovary renews her capacity for impregnation.

† For a fuller statement of this view, with illustrative examples, see p. 568.

tion, the latter phenomenon ought to be repeated whenever the former event occurs; and consequently in the case now under consideration M. Coste suggests that the same cause which provokes the discharge of the ovum in this case, also occasions fecundation, which arrests the menstrual flux before this has time to manifest itself.

Thus, if even the foregoing explanation could be deemed satisfactory, it appears necessary occasionally to fall back upon the old doctrine of the detachment of ova coincidently with fecundation, in order to supply the deficiencies of the newer theory of their spontaneous emission independently of it. It must however be confessed, that every view yet offered of the direct dependence of each separate act of menstruation upon a corresponding act of ovulation, disappoints expectation by leaving some condition relating to conception unexplained, or explainable only by raising an additional hypothesis; while many circumstances of common occurrence, such as the sudden reappearance of menstruation under mental emotion and the like, are left unaccounted for upon any hypothesis of ovarian dominance.

If next the ovular view of menstruation be tested by the evidence derived from anatomy, although many facts will be found in proof of the statement that ova are often emitted at the menstrual period, these cases have not been yet sufficiently collated to form a series capable of affording unquestionable conclusions as to the precise relation which the emission of ova bears to each menstrual act. That ova may pass spontaneously from the ovary during the menstrual flow is proved by cases already given at p. 567. and 605. M. Pouchet, however, supposes that it is the *maturation* of the ova which takes place during menstruation, and that their *emission* follows immediately or within four days after the cessation of the flow. M. Coste found the period of *rupture* of the Graafian follicle to be very variable. In one case the follicle was already burst on the *first* day of menstruation. In a second instance, although *five* days had passed from the cessation of the flux, the follicle was still entire, though the slightest pressure sufficed to cause its rupture. In a third case *fifteen* days had elapsed, and yet rupture had not taken place. In the example represented by fig. 380. *ten* days had passed since the last menstruation began, and the follicle was entire, though perfectly ripe, and apparently upon the point of rupture.

These examples, in the same degree that they favour a belief in the occurrence of impregnation at indefinite periods of the menstrual intervals, by showing how conception is then possible, discourage the view that the *emission* of ova is necessarily limited to the precise times of the menstrual flow. But until a larger number of examples than yet exists, showing the condition of the follicles during both the menstrual periods and intervals, has been collected and carefully compared, no definite conclusions as to the exact relation which the *emission* of ova bears to each act of menstruation can be arrived at, so far as anatomical evidence is concerned. For the attention of observers having been directed more to the condition of the ovaries at the time of menstruation than in the interval, much more has been ascertained of their state at the former than at the latter periods. Yet it is during the intervals of menstruation that conception in man normally takes place, while mammals become impregnated only during the œstrus.

It is important, therefore, to determine, thirdly, how far the œstrus or rut in the mammalia may be regarded as comparable with the act of menstruation in the human female; for if, as is commonly supposed, these two functions are identical, or nearly so, then the facts to be derived from comparative anatomy may assist further in determining the nature and extent of the relation between menstruation and ovulation in man. But if the phenomena attendant upon the rut do not, in all respects, coincide with those accompanying menstruation, the conclusions which are legitimately deducible from observation of the former function must not be too strictly applied to the latter.

In the mammalia the periods of emission of the ova from the ovary, and of their passage down the Fallopian tube, are undoubtedly coincident with the œstrus. It is only on these occasions that the female manifests an instinctive desire for copulation. She is then said to be in heat. The vulva is congested, swollen, and bedewed with an increased secretion, which is generally odorous, and is sometimes tinged with blood. This condition is of brief duration. At the longest it continues for a few days. But whatever be its duration it is the only period during which the female can be impregnated.

In the human subject the periodical return of congestion of the reproductive organs, the menstrual flow, and the corresponding spontaneous emission of ova, so far as this point has yet been ascertained by post-mortem examination, accord with the phenomena displayed by the mammalia during the œstrus. It is also believed that in some instances conception has taken place *during* menstruation*, a circumstance which is clearly reconcilable with the anatomical evidences already produced, and is so far in accordance with what normally occurs in the mammalia during œstruation.

But here the analogy ceases. And from this point onwards the more closely the two functions are compared, the more plainly does it appear that although the œstrus and menstruation possess many circumstances in common, yet the resemblance endures only for a certain period, more or less brief, while, after this is past, there follows in man an intermediate condition which is not only not comparable with the corresponding intermediate

* Some of the few authorities for this fact extant are quoted in the works of Pouchet and Coste, *loc. cit.*

state in animals, but is in many of its essential features the direct converse of this.

For, as already stated, in the mammalia usually by the time that the ovum has reached the uterine extremity of the oviduct, or has entered the uterus, the opportunity for impregnation is lost, the œstrus is over, and the animal refuses the male: all the conditions immediately necessary to procreation then pass away, and an interval of perfect inaptitude ensues, which is sometimes so remarkable that not only are no ripe ova to be found in the ovaries, but even the male organ ceases to secrete semen. In this series of recurrent periods, marked by irresistible impulse, alternating with total inappetence for congress, nothing is more evident than that each corresponds with an internal physical condition, of which it affords a most intelligible explanation. The appetency occurring and remaining only as long as congress would be fruitful; the inappetency returning whenever this would be necessarily infertile.

Now, with regard to the human subject, whatever may be *possible* during menstruation, yet essentially the intervals of the menstrual acts are the times of fertility in women. And the only question that can arise upon this point is, whether the power of conception extends over the whole or over a part only of this interval—a question that has been already considered.

In all that relates, therefore, to the coincidence of the ovipont with the œstrus of mammals, the evidence derived from comparative anatomy serves to strengthen the belief in a corresponding correlation between the emission of ova and the act of menstruation in the human subject. But in respect of the interval, the great divergence of the facts here displayed tends to embarrass and perplex rather than to elucidate the question as it relates to man. For it is precisely in this interval that all the circumstances occur which, for want of a consistent explanation, have often thrown a doubt over the whole theory of the direct dependence of menstruation upon ovarian influence; and in elucidating these points, comparative anatomy affords little or no help.

In taking a retrospect of these several facts relating to menstruation and its connection with a corresponding ovipont, an essential distinction should be made between the influence of the ovaries in determining the power of the uterus to perform the menstrual act, and any influence which they may have over the periodicity of that function. In all that relates to the former faculty, the power of the ovaries may be regarded as indisputably established. In much that is connected with the latter, there is obviously room for more information than we at present possess.

If each separate act of menstruation is determined by certain modifications periodically occurring in the ovary, it is probable that the essential part of the process is the *maturation* of an ovum within the follicle, while the process of its *emission* may be an accidental feature, not always occurring, sometimes happening spontaneously, and sometimes caused in the way already suggested, but having nothing necessarily to do with the menstrual act, although the time of its occurrence may materially affect the period of a resulting impregnation.

The purpose of the *flux* remains to be considered. If the quantity of fluid escaping at each recurrence of menstruation be estimated at three, or possibly five, ounces, and the process is repeated, without interruption from pregnancy, lactation, or disease, once in every lunar month, or thirteen times annually for thirty years, then an aggregate quantity of seventy-two pounds or nine gallons on the former supposition, or of a hundred and twenty-two pounds or fifteen gallons upon the latter estimate, will have passed from the system in the course of menstrual life, and, so far as this is composed of blood, will have been apparently entirely wasted.

It is difficult to arrive at a perfectly satisfactory conclusion regarding the purpose of this large loss. For the external escape of blood must be regarded as, to a certain extent, an accidental feature in the process of menstruation. That it is not essential to fertility, is proved by the fact that women sometimes, though very rarely, breed who do not menstruate; that the temporary suspension of the menstrual flow during lactation is no certain preventive of conception; and that, occasionally, young girls become pregnant before the menstrual age has arrived.

The blood which escapes is certainly converted to no positive use. No office can be assigned to it, such, for example, as has been suggested for the analogous escape of blood into the ripe ovisac — an effusion that has been termed the menstruation of the follicle.* But although the blood, after it has passed the uterine epithelium, is altogether lost, it may, by escaping, fulfil the negative purpose of affording relief to the congested capillaries of the uterus. For we find, from various kinds of evidence, that, at each menstrual period, all the uterine tissues become charged with a more than ordinary quantity of blood, and, therefore, with the materials necessary to those rapid growths which have been shown to commence as soon as impregnation has taken place. From the moment that the latter occurs, the mucous and other tissues of the uterus begin rapidly to expand, and the current of blood is diverted to new channels. There is then no overplus, until the whole cycle of generative acts, including lactation, is complete. The only observable break happens at parturition; but after the balance of the uterine circulation has been restored by the escape of blood at the time of labour, and by the lochia, there is again usually no redundance until the office of the mammary glands has ceased. Then, the activity of the ovaries recommencing, the periodical hyperæmia of the uterine vessels returns, and the overplus is emitted in the form of menstrual

* See p. 556.

blood. And thus, by each act of menstruation, the uterus is placed in a state of preparation for that profuse development of its tissues which impregnation may at any time of the succeeding interval call forth.

The office of the uterus in insemination.— After menstruation, which is to be regarded as a process preparatory to impregnation, the next office of the uterus is that of receiving the seminal fluid, and apparently of conducting it to the Fallopian tubes, by which again it may, in rare instances, be carried as far as the ovary. To this office the form of the uterus appears to be well adapted in all its parts. For, first, the cervix uteri is so constructed as to lie in the centre of the upper dilated portion or fornix of the vagina, into which it projects to a distance of 3—4‴. This dilated extremity of the vagina forms a pouch which receives the extremity of the intromittent organ, and in this receptacle the seminal fluid is deposited. But, on account of the natural position of the uterus, which lies in the axis of the pelvic brim, while the course of the vagina corresponds with that of the cavity and outlet (*fig.* 433.), the cervix uteri is so directed (downwards and backwards) as to cause the os uteri externum to be maintained in the very centre of this pouch, so that the seminal fluid will be retained in a situation in which it is most certain to flow through this orifice into the cervix.* But the cervical canal is traversed by numerous furrows, which will act as so many channels, conducting the semen to the internal os, while the dilated central portion of that canal (*fig.* 424.) serves the purpose of a second reservoir.

It may also be readily believed that the ejaculatory act on the part of the male will suffice to carry the seminal fluid thus far, although the impetus with which it is propelled having been checked by the constriction caused by the external os uteri, would hardly suffice to carry it much beyond the more narrow barrier existing at the internal os. Or if it should pass this second obstacle, the almost complete apposition of the walls of the uterus would prevent any considerable penetration of the semen further into the uterine cavity, so far as this is dependent on the act of ejaculation.

But this very apposition of the uterine walls may, in another manner, assist the onward progress of the semen, by inducing a kind of capillary attraction, such, for example, as will cause water to rise, to a certain distance, between two plates of glass placed in close contact. The rigid walls of the human uterus, which are normally in such close apposition that sections made in certain directions scarcely suffice to display any appreciable cavity (*figs.* 426. and 427.), seem admirably adapted to favour this gradual rise of the seminal fluid between them towards the Fallopian tubes; and thus a compensation is provided for that peristaltic movement, which, in some mammalia with a more intestiniform and less rigid uterus, appears, under the influence of the coitus, to affect alike the vagina, uterus, and Fallopian tubes*, and to suffice for the conveyance of the seminal fluid from one extremity to the other of the generative track.

The action of the cilia of the uterine epithelium cannot, in any way, contribute to this result, if those observations are correct which agree in assigning to them a movement such as would create a current from within outwards; for it is obvious that such a motion would tend to retard rather than to advance the progress of the seminal fluid towards the Fallopian tubes.

If therefore any other power is needed to account for this movement, it must be sought in the action of the spermatic particles themselves. For, little adapted as their motions appear to anything like onward progression, yet they have been observed to continue long after ejaculation, in the fluid found within the uterus and tubes, and even upon the ovary.† It has been also proved beyond doubt that by this power the spermatozoa penetrate the ovum itself‡, and therefore to it may be attributed a certain share in the progress of the seminal particles through the uterus towards the oviducts, although this may not be a very considerable one.

Finally, it is possible that in man and the mammalia some such remarkable property may be possessed by the spermatozoa as that which I have observed in certain annellides. If a portion of the contents of the testis of the common earth-worm (*Lumbricus agricola*, Hoffm.) be placed under the microscope between two slips of glass, in about ten minutes the whole mass is seen to heave and writhe with astonishing energy, the form of the movement being that of the peristaltic action of the intestines (*fig.* 459.). Everything in contact with the spermatozoa becomes ciliated by them, one end of the filament fixing itself while the other vibrates free. The result is, that if the body to which the spermatozoa attach themselves is fixed, such as the glass, or the margin of a mass of granules, a line of cilia is formed whose action creates a strong current, and everything movable is drawn into the vortex, and is seen drifting rapidly along. But if the body to which they attach themselves is movable, then this soon becomes clothed with spermatozoa,

* Dr. James Blundell has described a peculiar movement which he observed in the vagina of the rabbit, and which serves to explain the mode of introduction of the seminal fluid into the uterus:— "This canal during the heat is never at rest; it shortens, it lengthens, it changes continually in its circular dimensions; and when irritated especially will sometimes contract to one-third of its quiescent diameter. In addition to this action the vagina performs another," which "consists in the falling down, as it were, of that part of the vagina which lies in the vicinity of the wombs; so that it every now and then lays itself as flatly over their orifices as we should apply the hand over the mouth in an endeavour to stop it. How well adapted the whole of this curious movement is for the introduction of the semen at the opening it is needless to explain." —Researches Phys. and Pathol. p. 55. 1825.

* Blundell *loc. cit.*; see also p. 611. of this article.

† See this article, p. 607.

‡ Newport, Phil. Trans. 1853. Pt. II. p. 267.

whose free ends moving rapidly, cause the whole to rotate. A most remarkable object

Fig. 459.

Spermatozoa of Lumbricus agricola in motion and forming cilia. (*Ad Nat.*)

is thus formed, which continues for a considerable time in motion, clearing for itself a free area, and in this it revolves, whilst its revolutions are apparently assisted by the action of other spermatozoa, which, having attached themselves to the periphery of the cleared space, keep up a perpetual vortex, in which the central body is partly a passive and partly an active agent.*

Whether any similar effect is capable of being produced by the spermatozoa in the human subject, or how far this property may be general in spermatozoa, I am not aware; but the circumstance is altogether too remarkable to be passed over without mention here, as it may serve to explain how the onward movement of spermatozoa can, in some cases at least, be aided by this peculiar property of the spermatic filaments to attach themselves to surfaces with which they were in contact, and to clothe these surfaces with a fringe of cilia capable of producing the ordinary effects of cilia in motion.

The office of the uterus in gestation.— The process of gestation may be considered to commence from the moment that the ovum, which has been subjected to the fertilising influence of the male generative element in the Fallopian tube †, is received impregnated into the uterine cavity. If no such contact of the generative elements as is necessary to the development of the ovum takes place, then the latter suffers no further change beyond that slight alteration in its condition during its passage through the oviduct, which has been already described; and ultimately it becomes lost, probably suffering decomposition, but at least giving no evidence of its presence in the uterine cavity. But if the ovum has been fertilised, then commences that remarkable series of changes in the physical condition of the uterus whereby this organ is fitted for the protection and nutrition of the ovum during the usual period of forty weeks in which the latter is normally retained within its cavity. As these changes involve very considerable alterations in the form and composition of the entire uterus, as well as of its several parts, they have been considered as a part of that series of metamorphoses which the uterus undergoes in its progress from infancy to old age, of which a description has been already given, (p. 644.).

The office of the uterus in parturition.— The act of parturition, or that process by which, in normal cases, the product of conception, after due development, is spontaneously separated and expelled from the parent body, constitutes the last chief office of the uterus.

The labour process may be regarded as essentially a contest between two opposing forces, which are *resisting* on the one hand, and *propulsive* on the other. Resistance is necessary to preserve the fœtus in its place. Propulsion is requisite to detach and expel it from the parent body. The resisting force is chiefly passive in its operation. It is that which is offered by the membranes enclosing the fœtus, by the os and cervix uteri, by the soft parts lining and closing in the pelvis, and lastly by the osseous and ligamentous structures of the pelvis itself. Naturally, these are sufficient to counteract any tendency to the escape of the fœtus from the operation of gravity upon it, in various changes of posture, or under any impulsive movements of the parent body. Their combined resistance is such as to require the operation of powerful muscles to overcome them before the child can be expelled. This power is supplied by the uterus, aided subsequently by the diaphragm and other muscles, abdominal and pelvic. Labour constitutes the performance, and birth the end of the process, for the accomplishment of which in a natural manner the forces should be nearly evenly balanced. The preponderance of power being, however, at first, on the side of resistance, and finally on that of propulsion. Whenever the forces are thus proportioned, the act of parturition is, *cæteris paribus*, natural. Whenever they are greatly disproportioned, the process is abnormal; whether the error be on the side of too much resistance, or too little propulsive force. In these last two particulars may be comprehended the history of every unnatural labour in which the mechanism* is at fault.

* These observations were first made by me at the time when the late Dr. Martin Barry announced his discovery of the penetration of the ovum by the spermatozoa in the rabbit, and were communicated to him, and subsequently for publication to Prof. Owen, in whose lectures on the invertebrata this account appears. Lectures on the Comp. Anat. and Phys. of the Invertebrate Animals, by Richard Owen, F.R.S., 2nd edit. p. 257.

† See p. 609.

* The mechanical operation of the parts concerned in labour having been reserved for con-

When labour is about to commence, the uterus having previously taken a lower position in the pelvis, begins to contract gently, and often without pain, so that the only or chief evidence of its action is an occasionally recurring tension and hardness of the organ.

These contractions commence apparently at the cervix, so far as it is possible to analyse them, and travel onwards towards the fundus *: the whole organ soon becoming firm and resisting to the touch, and its upper part rising and assuming a more prominent position in the abdomen. This hardness and tension is occasioned partly by the rigidity of the whole fibre, in a state of tonic contraction, and partly by the resistance offered by the incompressible contents of the organ, for which there is no exit so long as the cervix remains closed.

The contraction having overspread the uterus, a sense of pain is now first felt; the pain, like that of cramp, being usually proportionate to the sensible tension and hardness of the organ.

After enduring for a time the state of contraction gradually subsides, and is replaced by one of relaxation. In subsiding, the contraction observes the same order as in commencing, the os and cervix yielding first, while the upper portion and fundus remain longest tense and hard. From this it results that the antagonistic force, exerted by the two extremities of the organ, not being throughout contemporaneously and equally employed, the excess of the fundal over the ostial contraction will represent the measure of the unopposed, and consequently efficient, propelling power.

The period of action is followed by one of repose, in which the organ remains relaxed, and no pain is experienced.

After an interval of variable duration contraction returns, and continues to recur in rythmical order, but with a gradually diminishing interval, while at the same time the contractions, especially at the fundus, increase in intensity and duration.

As a result of these successive contractions, the os and cervix slowly yield, and a portion of the fœtal membranes, containing some liquor amnii, protrudes, in the form of a pouch. This, as the os uteri becomes still further opened, is followed by the head or some other portion of the child, which, having entered the vagina, ultimately fills up the pelvis, and distends the perineum.

At this period the abdominal and pelvic muscles are brought powerfully into play. Their cooperative action is occasioned by the parts of the child occupying the pelvis irritating structures which are abundantly supplied by spinal nerves. And now the chief use of spinal reflex action, in relation to labour, becomes manifest, not so much in regard to the uterus itself, whose contractions are probably still mainly dependent upon its own sympathetic nerves, as in that correlation with other parts, between which and the uterus it is essential that consentaneous action should be occasionally established.

The powerful cooperation of the abdominal muscles, which form as it were an additional sheet of contractile fibre, nearly surrounding the uterus, being thus enlisted, the passage of the child is completed with greater rapidity and certainty; and, after a pause, the placenta and membranes are expelled, the liquor amnii having, either altogether or in part, escaped at some earlier period of the labour.

This general sketch of the operations of the uterus in labour will suffice as an introduction to a more detailed and critical examination of the nature of the forces employed, and of the manner in which these are called forth.

Of the peristaltic action of the uterus, and its cause. — From direct observation upon many mammalia, it is known that the action of the uterus is in them peristaltic, *i.e.*, the contractions commence at certain points, and pass on from segment to segment slowly, and in a vermicular manner. If a single point of an organ so composed is irritated, the action starts from the point of irritation, and spreads outwardly, and by irritating different points, other peristaltic centres may be obtained.

Although the human uterus does not admit of the same direct methods of observation which can be employed in animals, yet from all that is known, we may conclude that its mode of contraction does not differ in any important particular from that of other similarly constructed hollow muscles, when engaged in propelling or expelling their contents.

The principal circumstances bearing upon this point in regard to the human uterus are the gradual and slow contraction, followed by an equally slow return to a state of relaxation —phenomena easily observed, when the hand is placed upon the abdomen of a woman in labour—a certain tremulous motion of the os uteri, when contraction is commencing, followed by a sensible gradual hardening of the uterus, before the woman is herself conscious of pain; the longer abiding of the contraction at the fundus than at the cervix; and the occasional segmental contraction of the organ after labour, commonly termed *hour-glass contraction* *, which may occur at any point intermediate between the fundus and cervix, and which resembles similar contractions of common occurrence in other hollow muscles, whose action is peristaltic. These several circumstances, added to the general analogies, suffice to show that the action of the human uterus is peristaltic.

Peristaltic action, as it occurs in vertebrate animals, is found to depend upon the structure of the organ displaying it, rather than

sideration in a separate article (Parturition, Mechanism of, Vol. III. of this Cyclopædia), the vital endowments only of the uterus, as far as these relate to the parturient act, are here examined.

* Wigand, Die Geburt des Menschen. Berl. 1820.

* See p. 702.

upon the mode of its innervation or excitement. So that if in a situation where organic fibre is usually found, the intestine, for example, of *cyprinus*, the part is composed of striated muscle, then no organic or peristaltic action can be produced in it; but upon excitement, contractions of the kind usually seen in striated muscular fibre ensue.*

In the same way the peristaltic action of the uterus, although exhibiting certain differences, according to the manner in which it is evoked, is nevertheless to be referred to the peculiar composition of unstriated fibre, and not to the mode of innervation or excitement of the organ.

For the muscular fibre of the uterus is not bound up in separate sheaths, as voluntary muscles are, nor do the fibres run principally in one direction, nor are they long and continuous — conditions all favourable to that quick transmission of nerve influence, and rapid action which occur in voluntary muscle — but the fibre cells are for the most part distinct, lying in apposition, or imbedded in a matrix of amorphous tissue (*fig.* 436.), and forming by their combination intricate laminæ.

Through a tissue so composed, the influence of a stimulus can only be propagated slowly, and the organ formed of it can only contract after a vermicular or peristaltic manner. Nevertheless, the power, the endurance, and the orderliness of the action that ensues, will be, to a certain extent, dependent upon the nature and mode of application of the excitant. It cannot be questioned that, under many circumstances, the direct application of a stimulus to the uterine muscular structure excites its contractions in the same manner that the food does those of the œsophagus and intestines, without any intervention whatever of nerve. This happens when the hand is passed into the bare uterine cavity after labour, or when the membranes are separated from the inner surface of the uterus by a catheter.

To bring such an organ into *co-ordinated* action, all that appears necessary is, that nerve fibres should enter its tissue at a certain number of distinct points or centres, whence the irritation excited at these spots being propagated from fibre to fibre, may spread through the mass, until the whole is brought into harmonious operation.

And it need not excite surprise if these centres of excitement are few, and the nerves of the gravid uterus consequently not numerous; for a more abundant supply of nerve force, and more rapidly recurring contractions, would be prejudicial in labour, by bringing the uterine walls more constantly and violently into contact with the fœtus, and by driving out the blood passing through them so rapidly as to cause dangerous regurgitation, or so frequently as to produce fœtal asphyxia, through too constant interruption of the placental circulation.

* Weber, in the article *Muskelbewegung*, in Wagner's Handwörterbuch. 1856.

It is in favour of the views of Wigand, who maintains that uterine action begins at the cervix, and travels upwards, that the cervix receives a larger supply of nerves than the fundus, so that the action may be here first established, and the fundus afterwards excited. But however this may be, it is known that unless all parts of the organ are eventually brought into consent, the labour does not proceed regularly, for if one portion is felt to be hard, and another at the same time soft, irregular action and spurious pains ensue. To ensure, therefore, consentaneous action between the respective points of the uterine fibre at which the nerves enter its tissue, and to establish and regulate the movements, appear to be the offices of the nerves in relation to the uterine structure.

Of the rythmic action of the uterus, and its cause. — The uterus, like the heart and the respiratory muscles, is time-regulated or rythmic in its action. In this action the usual three rythmic periods are noticeable, viz., a period of contraction, a period of relaxation, and one of repose.

The sensible phenomena which accompany the first period are, a gradually increasing and sustained hardness of the uterus, a gradual approach and continuance of suffering, and, after a time, a certain advance of the presenting part of the child. These occurrences do not commence coincidently, but each overtakes the other in the order enumerated.

The phenomena of the second period are, the gradual subsidence of the hardness, the gradual passing away of the pain, and the retiring of the presenting part, and these are more nearly coincident than the former.

The third period is marked by an absence of all sensible signs.

These three periods together constitute the uterine rythm, which observes certain laws, that are in some respects different from those which govern the rythmic action of other parts, as for example, of the circulatory and respiratory organs respectively.

In the action of the uterus, the repeats take place more slowly than in either of the instances just named, although between these two, also, there is a proportionate difference, nearly, or quite as great. The heart's rhythm being quickest, the respiratory rythm slower, and that of the uterus slowest of all.

But the rythm of the uterus does not observe a constant or uniform rate. At the commencement of labour, the order of sequence of the rythmic motion remains for a time tolerably constant; but as the process advances the rythm becomes modified, so that, like the example of the heart under violent emotion, the interval shortens, while the force and vigour of the contractions increase.

It is a matter of great interest to discover, if possible, the determining cause of this rythm; that which constitutes the regulating as well as the disturbing force. The latter should be rather termed the accelerating force, for it is beyond question a healthy necessity which, for the purpose of advancing the process, demands this graduated change of the uterine rythm throughout labour. Rythm plainly does not, like peristaltic action, depend upon the structure of the organ which displays it, for the three examples here taken, viz., respiratory muscles, heart, and uterus, differ from each other materially in composition. The first consists of striated voluntary fibre; the second of striated involuntary fibre; the third of unstriated involuntary fibre. It may therefore be concluded, that something else than structure determines rythm. This appears to depend rather upon the manner in which the contractions are evoked, and hence upon the mode of innervation, which is different for each organ. The heart and respiratory muscles each admit of more easy observation than the uterus, and referring to them for aid in the elucidation of this question, we find that each of these organs, or sets of organs, is provided with a nervous rythmic centre, upon which its rythm depends, and upon the injury or destruction of which the rythm immediately ceases, — the rythmic centre of respiration being in the medulla oblongata, and that of the heart in its own proper ganglia. Which of these divisions of the nervous system furnishes the rythmic centres of the uterus has not been determined, but from the analogies just quoted, we may select by preference the heart, because its actions most nearly resemble those of the uterus, in being purely involuntary, while the case of the respiratory muscles constitutes an example of mixed movements wherein volitional can be superadded to unconscious rythmic motion.

If therefore the rythmic action of the uterus is regulated in like manner with that of the heart, we must, upon the strength of this analogy, look for its rythmic centres among the sympathetic ganglia which lie nearest to the organ.

And this view does not necessarily exclude a certain influence of the spinal nerves over the rythmic action of the uterus. For just as under emotion or bodily excitement both the cardiac and respiratory rythms are accelerated, so, as labour advances, and more parts become irritated, the uterus appears to receive an addition of nerve force which may be possibly acquired from other and more distant centres than its own proper ganglia.

The heart's rythmic centres have been regarded by some physiologists as so many "magazines" of nerve-force, whence at regulated intervals this force is discharged, causing the muscular structure to contract in accordance with the rate of supply of the stimulus. The influence of these nerve-centres is best shown by placing a ligature upon them, or by cutting them away. When hindered in their operation by tying, the *rythm* ceases, though the motor power is not lost. When they are cut away, together with certain portions of the heart, the other portions cease to have rythmic motion, though they may still be artificially excited to repeated single actions.*

But an inconstant stimulus thus furnished to the muscular structure being powerless to produce a permanent or tonic contraction, the effect after a short time passes away to be reproduced upon a fresh application of the excitement. In this way rythm, so far as it is dependent upon nervous supply, is apparently determined.

But in the case of the uterus we observe that the *rate* of the rythm must be to a certain extent limited by the peculiar nature of the uterine fibre. For this, as already shown, is of a kind which cannot be excited to *rapidly repeated action* like the heart. In this form of fibre the response to the stimulus is slow, and often does not take place until after the excitant is withdrawn. Hence the meaning of that slow repetition of uterine action which is observed in ordinary labour.

When this point is further examined, it will be found that, according to the degree or kind of excitement employed, the uterine rythm may be merely accelerated, or a rythmic may be converted into a more continuous action. The influence of the passage of the child during labour over successive surfaces in quickening uterine action has been already shown. Another example may be drawn from the effects of ergot. When ergot is given by the stomach some time usually elapses before the ergotine mixes with the blood sufficiently to excite the rythmic centres, but that being done, the action is simply augmented, or else occasionally it becomes so violent that the intervals are obliterated, and one contraction becomes merged in another, so that an intermittent is converted into a continuous uterine action.

But that which more certainly demonstrates that the rate of the motions, whether rythmic or constant, is dependent on the kind and extent of irritation, is the variation in the results obtained by different modes of inducing premature labour. If, according to the method of Kiwisch, water is injected simply against the cervix, after several repetitions, rythmic action is slowly excited. If the cervix is distended by the introduction of a sponge tent, rythmic action ensues more quickly and certainly. But if the first proceeding is so varied that the water, instead of being merely thrown against the cervix, is introduced between the membranes and the uterine walls for a very short distance, so as gently to effect their separation from the inner surface of the uterus, labour is induced with greater certainty and speed than in any other way; but should the separation be carried still further, some such tumultuous form of labour results as ergot produces when acting in the manner just specified. The uterus acting continuously and very energetically rather than intermittingly.

Influence of the different nervous centres upon the uterus in parturition. — In the present unsettled state of neural physiology, especially in

* Paget, Croonian Lecture; Proceedings of Roy. Soc. vol. viii. No. xxvi. 1857.

relation to the powers of the different nerve centres, it is scarcely possible to arrive at any satisfactory conclusion regarding the relative degrees of influence which these may be supposed to exercise over the movements of the uterus. The marked differences of opinion still existing upon this subject* afford sufficient evidence of the uncertainty of the data upon which definite conclusions can be based. In this uncertainty, however, all points of the nervous system are not equally involved.

The amount of influence of the cerebrum upon the act of parturition can be determined with tolerable accuracy. That the uterus is in communication with the brain is proved by the fact that the woman is conscious of the fœtal movements, and that she suffers pain when the uterus contracts. Emotion may excite, and may also for a time delay, uterine action. The will cannot operate directly upon the uterus, either in the way of producing, or of restraining its contractions, but a slight indirect influence may be occasionally perceived, when by voluntary changes of posture, or by the use of those muscles which assist labour, the force of the uterus is slightly increased; or conversely, when, by carefully restraining all such movements and actions, this result is avoided.

It is further shown by the occurrence of labour in cases of complete paraplegia, and also during states of unconsciousness, induced by anæsthetics, that the uterus contracts while it is withdrawn from all volitional and like cerebral influences.

These several examples serve to show to what extent the contractions of the uterus may be influenced by the cerebrum, and also how that influence may be withdrawn. It is obvious that psychical influences are neither necessary nor accessory to the simple act of labour. They may often be regarded as disturbing, but not as regulating forces. Hence the dominant power over the contractions of the uterus, which is exercised during labour, must have its seat in some of those nervous centres that are placed lower than the cerebrum.

We may therefore proceed next to inquire what are the attributes which from direct observation and analogical reasoning the uterus may be supposed to derive respectively from the ganglionic and spinal systems, regarded as separate sources of motor power. But here, on account of the intimate manner in which the nerves derived from each of these centres are bound up together, great difficulty arises in distinguishing between the operations of each, and these difficulties can be only in part surmounted.

The circumstances which point more particularly to the influence of the ganglionic system will be first considered.

The uterus derives a greater proportionate supply of nerves from the ganglionic than from the spinal system. This appears from the researches of both Snow Beck and Kilian. The actions therefore of those parts or organs having like endowments, which are in other respects also comparable with the uterus, may be here examined.

Of all organs the heart is that which most nearly resembles the uterus. It constitutes, after the uterus, the largest hollow muscle. Like the uterus, it acts with rhythm, and, in a certain degree, peristaltically. It continues its contractions, with little, if any, interruption, for a long time after its principal cerebro-spinal connections have been destroyed, as by tying the pneumogastric nerves. It continues to contract rhythmically in many animals for a variable time after death, or when cut out of the body Its contractions are regulated mainly by sympathetic ganglia, while the cerebro-spinal fibres which it receives serve to establish relations between it and other parts.

The uterus exhibits many like peculiarities. It acts with rhythm and peristaltically. It continues these actions, in numerous species of animals, for a variable time after death. Even in the human subject, a post-mortem power of contraction seems to be occasionally retained, as in the case of women whose spontaneous delivery has taken place some time after all evidences of somatic life have ceased.* In these several offices we may conclude that the uterus also, so far as its operations are under the dominion of the nervous system, is, like the heart, chiefly influenced by sympathetic ganglia and nerves.

That this is the case is also further shown by the occurrence of delivery under circumstances in which *all* spinal influence appears to be abrogated. The following is an example.†

A woman was attacked with paraplegia in the eighth month of pregnancy. She had neither sensation nor motion in any part below the umbilicus. No reflex movements whatever could be produced by tickling the soles of the feet. The fæces passed involuntarily, and the urine was drawn off daily. About the ninth month, her medical attendant, when about to pass the catheter, found a full-grown fœtus in the bed (dead). The uterus was contracted, and the placenta in the vagina. The

* See *Tyler Smith*, Parturition and the Principles and Practice of Obstetrics; and Lancet, 1856. *Scanzoni*, Lehrbuch der Geburtshilfe. *Brown-Séquard*, Physiology and Pathology. *Carpenter*, Principles of Human Physiology; and *Todd*, art. Nervous System, in this Cyclopædia.

* A large number of these cases has been collected by Dr. W. H. Wittlinger, "Von der nach dem Tode der Mutter von selbst erfolgenden Geburt," in the Analekten für die Geburtshülfe, Bd. I. 1849. All cases of *post-partum* delivery are probably due to one of three causes, viz., to a contractile power or irritability remaining in the uterus after death, and comparable to that which in voluntary muscles produces the now well-known *post-mortem* cholera movements; to *rigor mortis;* or to the development of gases within the abdomen or uterus, causing the expulsion of the child by pressure. The first is probably the cause of birth within a few hours, and the last several days, after the death of the mother, and the second of the expulsion of the fœtus before decomposition has set in, yet at a later period than can be accounted for upon the first hypothesis.

† For this case I am indebted to Mr. Paget.

woman was entirely ignorant of what had occurred. Scanzoni and Chaussier relate similar examples of birth taking place notwithstanding complete paralysis of the sensitive and motor functions of the lower half of the body. In Chaussier's case the pressure was occasioned by a hydatid cyst which involved the chord on a level with the first dorsal vertebra.*

On the other hand, that the uterine movements are also *capable* of being influenced by spinal fibres, appears from the following considerations. Uterine contractions may be excited by the application of cold to the general surface of the body, or by placing the child at the breast; by injecting warm and stimulating fluids into the rectum, and in other like modes.

Again: the uterus, under various circumstances of health and disease, is observed to react upon all or several of the parts just named.

Hence it appears that a mutual relationship is established, by virtue of which the uterus may be either the excitor of actions in these parts, or may through them be itself excited to action. And there can be no doubt that the spinal cord is the agent through whose reflex operations these several effects are produced.

From this evidence it may be concluded that the double supply of nerves answers different purposes. That the *spinal* system furnishes nerves for the purpose of bringing into harmonious relations all those organs whose cooperation with the uterus is essential or accessory to various steps of the reproductive process. While the organ deriving also a similar or even larger supply from the *ganglionic* system, these nerves serve to regulate the functions which the uterus itself is capable of discharging without cooperative aid. In this view the offices of the spinal system, as a system of relations, and of the ganglionic, as a system presiding over the direct acts of the parts which it supplies, may be separately exhibited. It is doubtless also a chief office of the ganglionic system to regulate and control the action of the blood-vessels with which the uterus is so largely supplied.

What is the exciting cause of labour?— This question carries us only one stage further in the preceding course of inquiry: and the reply to it will be nearly found in the facts already stated. For if these serve to throw light upon the causes of the rhythmic and peristaltic movements of the uterus, then the conditions which determine the first rhythm and first peristalsis, or, in other words, the beginning of labour, cannot lie very remote from these.

Many circumstances may evoke the first rhythm, which being followed by others, labour becomes established. Thus, irritation of incident nerves in various parts and organs may so force those sympathies with the uterus which, for other uses, are established by the spinal system of nerves, as to bring on an unnatural and premature form of labour; — but this is not the present question.

The determining causes of natural labour can be only satisfactorily sought among that class of phenomena which causes the separation of the ripe fruit from the stem which bears it: in a perfecting, namely, of the fruit or product of conception, so that it becomes fitted for an independent existence, and as a step preparatory to this, in a gradual metamorphosis of those tissues which, having served for a time the purpose of connecting the two together, are now no longer required by either. This connecting medium in the human subject is the decidua, which lines the whole uterus. Its metamorphoses during pregnancy have been described. Already as early as the middle of that period, the preparation has begun for a new tissue, which, after labour, is to reconstruct the lining membrane. The old attenuating and perishing decidua, now no longer needed, except at the spot where it

* Cases of paraplegia have sometimes occurred in which artificial aid appears to have been needed to complete the delivery, as in a case cited by Brachet (Fonctions du Système nerveux ganglionaire, p. 266. 1830). By those who contend for a preponderance of spinal influence over labour, such cases are cited in proof. It is said that notwithstanding the complete loss of sensation and motion in the extremities, independent reflex operations may still be preserved in the uninjured portion of the chord. But the motions which may be occasionally excited by irritating paralysed limbs are "disorderly and purposeless," and are in no way comparable with those co-ordinated actions that characterise natural labour. Moreover, the argument is entirely inapplicable to the case cited in the text, in which no reflex action whatever could be produced. It has also been supposed that an essential distinction may be drawn between cases in which the disease is situated high up, and those in which it occupies a lower situation: in the latter cases the portion of chord supposed to furnish spinal nerves to the uterus being involved in the disease, and in the former not. But such conclusions can be of little value until the precise limits of the chord, whence spinal fibres can be derived to the uterus, have been anatomically determined. (See the account of the origin of these nerves at p. 641.)

For like reasons it does not appear that in the present state of neural physiology in relation to the uterus, satisfactory conclusions can always be drawn from experiments upon animals. For although it might seem probable that in a case of mixed nerves, by destroying the centre or origin of one of the sets, the functions of the other might be left unimpaired; or by stimulating one of the nerve centres alone, their actions would be exclusively called forth, while the rest would remain passive; still, absolute conclusions cannot always be arrived at, even in these ways. For in the latter case, on account of this very intermixture of nerves, whenever we attempt to stimulate ganglionic centres, or plexuses, we are dealing at the same time with the spinal fibres which pass through them. Or contrariwise, when we endeavour to destroy extensive tracks of spinal centres, we do not know if the arrest of labour that may follow is not due to the violence which, in most of these experiments, has caused the death also of the animal within a few hours or days after, rather than to the destruction only of the portion of spine whence uterine fibres are supposed to be derived. In this way, perhaps, we can explain those discordant results of experiments, in some of which labour has been arrested, and in others has not apparently been interfered with, so far as uterine action alone is concerned, after greater or less injury or destruction of the chord.

covers the placenta, loses by degrees the character of active vitality, and its tissues are converted into molecular fat.

Other and corresponding changes, of which an account will be hereafter given (see PLACENTA), occur in those structures in which the fœtal blood circulates. The profusely developed capillaries which ramify within the villi during the early and middle periods of gestation begin to suffer retrogression as the time of separation approaches, and the fœtal blood flows in more simple and relatively fewer channels, while, not unfrequently, entire villi become obliterated by calcification.

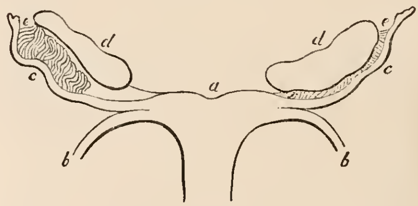
While these changes are proceeding in the temporary structures that serve to connect the fœtus with the uterus, structures which begin in part, at least, to become effete, even before the offices for which they are formed have been fully carried out,—the tissues which are to be employed in the process of expulsion are as yet only ripening into full strength, although they also, in turn, are about to suffer a like retrogression, but not until the object of their formation has been accomplished. The contractile fibre, which constitutes the principal portion of the uterine tissue, has gradually, during pregnancy, advanced to that more complete form which is reached commonly about the sixth month. From this period probably no new development of muscular fibre takes place, although that which is already formed appears to increase somewhat in size and power. It constitutes now a contractile tissue, capable of exerting great expulsive force. How easily, and in how many ways, the contractile power may be evoked, has been already shown. It is probable that by the series of metamorphoses already enumerated as occurring in the parts which connect the fœtus with the uterus, the entire ovum becomes gradually placed in the position of a foreign body within that organ; a position which may be compared to that of the food within the alimentary canal. And just as the food is propelled onwards, peristaltically, by irritation of successive portions of the containing surfaces, until, with the subsequent cooperation of muscles acting under the dominion of the spinal cord, it becomes finally ejected; so the ovum is itself apparently the excitor of those first peristalses in the uterus which initiate labour. How these become coordinated and established, and how the rhythmic periods are probably determined, has been already considered, as well as the means by which, during the further advances of the child over successive portions of the generative track, other nerve and motor forces are added to those with which the process commenced.

ABNORMAL ANATOMY OF THE UTERUS.

A. *Defective development.* — Imperfect or defective development of the uterus may occur under two circumstances. There may be either an original defect in its organisation, arising from a failure of growth or imperfect formation of those portions of the generative canal out of which the uterus is developed; or else the organ, having been regularly formed during embryonic and fœtal life, may not have proceeded in its development, but may have retained the infantile character after the usual age of puberty has arrived and passed.

1*st Class. Congenital defects.* — Defects of this class may affect the uterus alone, or may be conjoined with corresponding imperfections of other organs. In order that their nature and origin, as well as the possibility of their occurrence, independently of any malformations of the other reproductive organs, may be clearly understood, it is necessary to remember the mode in which the uterus is originally constructed. Formed by the coalescence of

Fig. 460.



The entire internal generative organs, from a fœtus of three months. (*After J. Müller* × 8.)

a, uterus; *b*, round ligaments; *c*, Fallopian tubes; *d*, ovaries; *e*, remains of Wolffian bodies.

the inferior extremities of the ducts of Müller*, the uterus will be materially modified in its construction according to the degree of perfection of those ducts, as well as by the amount of union which has taken place at their lower terminations.

Taking these particulars as affording a basis for classification the malformations of the uterus which are dependent upon original vices of formation may be arranged in four groups, viz.: —

Group 1. The ducts of Müller being both imperfect or undeveloped, there results a more or less complete absence of the uterus. The examples of total absence of the uterus which have been recorded are probably cases in which the rudiments exist, but have been overlooked, on account of their slight development; for generally there may be traced a more or less distinct fold of peritoneum lying behind the bladder and representing the broad ligament, within which are found some indications of a uterus. These rudiments consist of two uterine cornua, either conjoined at their lower extremities, or remaining separate in their whole course. They usually occur under the form of two hollow rounded cords or bands of uterine tissue, extending upwards towards the ovaries, and united perhaps at the usual seat of the uterus by cellular tissue, with which some uterine fibres are intermixed. Sometimes one or two little masses of uterine tissue are found. These are either solid, or they contain a small cavity

* See p. 642.

lined by mucous membrane. This constitutes the condition designated by Mayer the *uterus bipartitus*. The concomitants of this condition may be a short vaginal cul-de-sac, together with rudimental Fallopian tubes, and perhaps well developed ovaries. In the latter case the external organs may be well formed, and there may be no deficiency of sexual character, or the vagina may be entirely wanting.

The coexistence of this rudimental uterus with ovaries well developed is easily explained. For the ovary is formed out of a separate portion of blastema from that from which the Wolffian bodies and excretory duct of the generative apparatus are developed, *fig.* 400. and 416., so that the failure in growth of the one does not necessarily involve a corresponding defect in the other.

Group II. If one uterine cornu retains the imperfect condition last described, while the second undergoes development, the one-horned uterus or *uterus unicornis* is produced. So that the organ here consists of a developed and an undeveloped half combined.

The developed uterine horn may be either the left or the right. It then consists of a cylindrical or fusiform canal or body, curved outwardly in the form of an arch which exhibits various degrees of deflection from the meridian. To its upper extremity is usually attached a tube leading to the seat of a well-formed ovary.

The second or undeveloped cornu, with its tube, is not always entirely deficient ; but there often exists a rudiment in connexion with the developed horn, which, according to the degree of malformation, is either solid or hollow, or is traversed by a canal opening into the cervix of the developed half.

In the case of the uterus unicornis, notwithstanding the imperfection of one uterine half, both ovaries may be found alike developed.

The type of this condition of uterus exists as a normal formation in the class aves, where one side only of the generative apparatus proceeds in its growth, and the other remains undeveloped from an early period of fœtal life.*

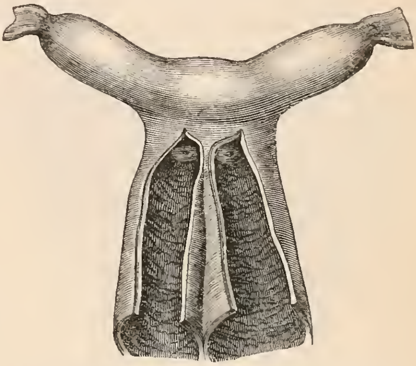
Group III. If, instead of an unsymmetrical growth of the two uterine cornua, such as occurs in the last example, both sides are alike developed, yet without any, or with only an imperfect, junction of their lateral borders there is produced a *uterus bicornis*, falsely termed a double uterus (uterus duplex). Here however there is no evidence of plurality, or true duplicity of the uterus, but only a deficiency of that union of the two separately formed halves by whose subsequent conjunction the organ is normally constituted.

This conjunction should naturally commence from the level of the point of attachment of the round ligaments, and the variations in the degree of malformation will be according to the height at which the union of the uterine halves stops short of that point.

The highest degree of malformation in this group, or the greatest departure from the normal form, is that in which the two uterine halves do not coalesce at all, but remain completely divided in their whole extent. This happens very rarely, and is co-existent with other malformations, such as fissure of the abdominal and pelvic walls. The division is here so complete that certain of the pelvic or abdominal viscera may occupy the space between the two uterine halves.

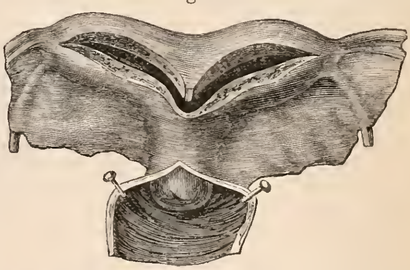
In the next degree of this kind of deformity a horizontal commissure occupies the angle in which the two uterine halves meet, and serves to unite them together (*fig.* 461.). The horizontal commissure is composed, like the cornua, of uterine tissue, and represents the fundus uteri. According to the height at which it is placed, the external form of the uterus approaches or recedes from the normal type. Rokitansky* has pointed out how the situation of this commissure affects the angle in which the two cornua meet, and consequently the relative mutual position of the two uterine halves. The nearer the point of co-

Fig. 461.



The body of the uterus divided into two halves, which are united at the cervix by a horizontal commissure representing the fundus. The os uteri and vagina are double. (After Busch.)

Fig. 462.



The vagina, os uteri, and cervix, single. (After Busch.)

The body of the uterus forming two cornua, which are still nearly horizontal, but are united by a commissure at a higher point than in *fig.* 461.

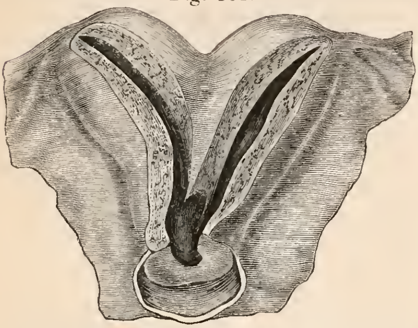
* See Fallopian tube, p. 613.

* Loc. cit. p. 274.

alescence of the two halves approaches to the external orifice, the more obtuse will be the angle at which their junction takes place, and the more extensive will be the fissure (*fig.* 461.). On the other hand the higher the point of union, the more acute will be their angle.

This becomes obvious in the lesser degrees of deformity represented in *figs.*462. and 463. In *fig.* 462., although the commissure is placed at a higher point than in *fig.* 461., so as to be much further removed from the external os, there is still a considerable separation of the two cornua, and their direction is still mainly horizontal ; but in *fig.* 463., where a more perfect coalescence of the two halves has taken

Fig. 463.



The cornua more completely united externally, and the two halves becoming more nearly parallel. (*Ad Nat.*)

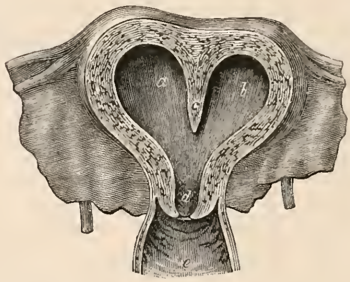
The body is still divided by an internal septum which descends from the commissure as far as the commencement of the cervix, where it ends in a thin falciform edge.

place, and, consequently, where the commissure approaches nearer to the points of attachment of the Fallopian tubes and round ligaments, the angle has become so much smaller, that the two halves begin to lie nearly parallel with one another, and the horns, or ununited portions, exhibit only a slight divergence.

In this, as well as in the following group of malformations, there often proceeds from the commissure an internal septum which descends to a variable depth, and exercises a corresponding influence upon the separation of the two halves. In cases where the commissure representing the fundus lies very low, there may be no septum, and a single cervix conducts into two uterine halves which lie right and left of it. In cases where the fundus is higher, if the septum extends downwards only in a slight degree, as in *figs.* 462. and 464., the cervix is still common to both sides of the uterus. Where the septum begins to divide the cervix, as in *fig.* 463., the separation of the two uterine halves is more complete, but there is still a common os externum, leading to the two canals. The highest degree of division, and consequently lowest type of structure, is that in which the septum extends not only through the cervix, but even to the extremity of the vagina, dividing the latter, *fig.* 461., together with the hymen in the virgin state, so that there are two complete canals leading to corresponding uterine halves.

Group IV. In this group the external form of the uterus differs but little from the normal character. The breadth of the organ, especially between the points of entrance of the Fallopian tubes, is usually greater, and the fundus, though arched, is more shallow than usual. Here also a slight notch, extending into a shallow furrow, running along the posterior uterine wall, may indicate the seat of that internal vertical septum which more or less completely divides the uterine cavity into two halves, and constitutes the *uterus bilocularis* (*fig.* 464.).

Fig. 464.



The body of the uterus showing only a slight indentation externally. (*After Busch.*)

An internal septum *c*, divides it into two loculi, *a* and *b*. The cervix, *d*, is single.

The extent of this septum, and consequently the more or less perfect formation of two separate loculi, exhibits the same varieties as in the former group. The partition may stop short at the cervix, or extend in rare cases completely through that canal, and even divide the vagina. Where the septum is rudimental, and extends only to the cervix, the lower free border is usually thin and falciform (*fig.* 463.), having its concavity directed forwards, the lower extremity being that which is connected with the posterior uterine wall.

These several deviations from the normal form of the uterus will more or less influence the manner of performance of all its functions.

The acts of *menstruation* and *insemination* are those perhaps which are the least disturbed. Regarding this former function, wherever the ovaries are perfect and a channel exists for the menstrual fluid, as, for instance, in the one-horned uterus, the external escape will occur as usual ; but in the case of atresia of the vagina, and in those examples of a hollow rudimental uterus, the menstrual blood collects, and distending the closed sac forms there a hæmatometra.* Where the parts representing the uterus are entirely solid,

* See p. 697.

the menstrual molimen may not be thereby hindered, but the escape of blood can only take place, if at all, from some unsuitable situation producing the so-called *menses devii*, or vicarious menstruation.

Regarding the influence of these malformations upon insemination and a resulting impregnation, much of necessity depends upon the condition of the vagina; for this canal may be in so rudimental a state as not to admit of intromission. The canal leading to the ovary also may be either open or closed. In the case of the rudimental tube attached to one side of a single developed cornu, the passage may open into the cervix of the developed half, and thus a channel for the seminal fluid will be established in connexion with an ovary that may be normally formed, and thus impregnation and gestation, even in an undeveloped cornu, is possible.*

Greater difficulties and considerable danger indeed to life arise, during the progress of *gestation*, in the higher deformities of this class. Pregnancy in a rudimental horn would probably be attended by rupture and fatal hæmorrhage at an early period, as happened in Rokitansky's case quoted in the last note, and as usually occur also in the not dissimilar example of ordinary tubal gestation. But even in the case of pregnancy occurring in the developed horn of a uterus unicornis, the undeveloped half will exercise a marked influence upon the progress of gestation, by impeding the due expansion of the developed side; while the supply of blood usually furnished in pregnancy being here provided by only one set of vessels, the course of the pregnancy will probably suffer in a corresponding degree.

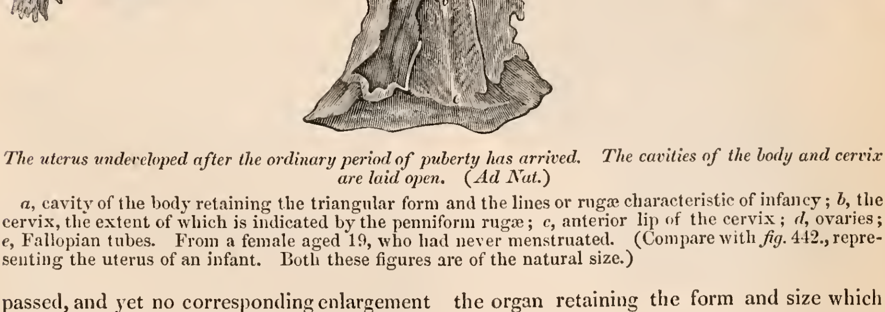
In the cases of the uterus bicornis and bilocularis, either horn, or either uterine half, may become separately or alternately the seat of gestation, or pregnancy may proceed simultaneously in both. There is even reason to suppose that twins have been developed in one half, and also that superfœtation has obtained in such a condition of parts.

In those cases where the vagina is partitioned into two canals impregnation may take place more frequently or even exclusively on one side, in consequence of the one channel or half being more favourably formed for intromission than the other.

Regarding the influence which these anomalies may have over the last office of the uterus, viz. *parturition*, it is only necessary to observe that in both the uterus bicornis and bilocularis the organ will be deprived of the advantageous use of the fundus, which so materially aids expulsion in a normally formed uterus, while in the case of the uterus unicornis and bicornis, where the impregnated half usually forms an acute, or even nearly a right angle with the axis of the body, the effect, as Rokitansky has shown *, will be, that during the act of parturition the axis of the impregnated half meeting with the vaginal axis in an obtuse angle, the direction of the uterine force and of the expulsion of the fœtus will cross the axis of the pelvis, and fall upon the pelvic parietes that lie opposite to the vertex of the pregnant half of the womb, and thus the act of parturition will be rendered correspondingly difficult in such cases.

2nd Class. Defective development after birth. The pre-pubertal uterus. — The ordinary age of puberty may have arrived and

Fig. 465.



The uterus undeveloped after the ordinary period of puberty has arrived. The cavities of the body and cervix are laid open. (Ad Nat.)

a, cavity of the body retaining the triangular form and the lines or rugæ characteristic of infancy; *b*, the cervix, the extent of which is indicated by the penniform rugæ; *c*, anterior lip of the cervix; *d*, ovaries; *e*, Fallopian tubes. From a female aged 19, who had never menstruated. (Compare with *fig.* 442., representing the uterus of an infant. Both these figures are of the natural size.)

passed, and yet no corresponding enlargement or growth of the uterus may have taken place; the organ retaining the form and size which

* See a remarkable case of pregnancy in the rudimentary half of a uterus unicornis, ending in rupture of the sac and death in the third month, by Rokitansky. (Pathol. Anat. Syd. Soc. vol. ii. p. 277.) The preparation is preserved in the Viennese Museum.

* Loc. cit.

characterise it in infancy or childhood. Such may be the condition of the entire internal organs, as in the accompanying example (*fig.* 465.) of the undeveloped uterus from a female aged 19, who had never menstruated. In these cases, the body generally exhibits a corresponding feebleness of growth, and the sexual attributes are little, if at all, displayed.

The infantine condition of the uterus is here exhibited in every particular. The proportionately large size of the cervix, *b*, the small triangular uterine cavity, *a*, with a raphé extending into it, and the thin parietes, are precisely such as are usually found in the infantine organ.

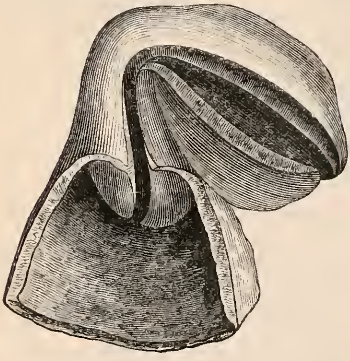
In the last case, the ovaries exhibit also their ordinary infantine proportions; but these may become developed, and the functions of menstruation may proceed naturally, while the external characteristics also are those of a well-formed female, but the uterus remains small, the vagina is short, and instead of terminating in the usual fornix, with a projecting cervix, this canal ends in an aperture, which just admits a sound or probe, and is not furnished with the usual lips of the os tincæ. These cases usually result in sterile marriage, and may be easily detected during life.

Anomalies of form. — Deviations from the ordinary form of the uterus which are acquired during life, and do not proceed from original malformation, or imperfect development, such as that last noticed, will be here considered.

The angular flexions of the uterus which take the definite forms of a forward or backward curve, or of an inflexion towards either side, are distinguished as anti- and retroflexion and lateral inflexion.

a. Antiflexion of the uterus is that condition of the organ in which, without any material change of position in the cervix, the body is bent forwards, so that the fundus, lying more or less horizontally, is directed towards the symphysis pubis, while, according to the degree of inflexion, the anterior wall of the uterus is brought near to, or in contact with, the cervix in front, while the posterior wall looks upwards, corresponding more or less with the plane of the pelvic brim. The point of curvature is always at the line of junction of the body with the cervix uteri, and here an angle more or less acute is formed.

Fig. 466.



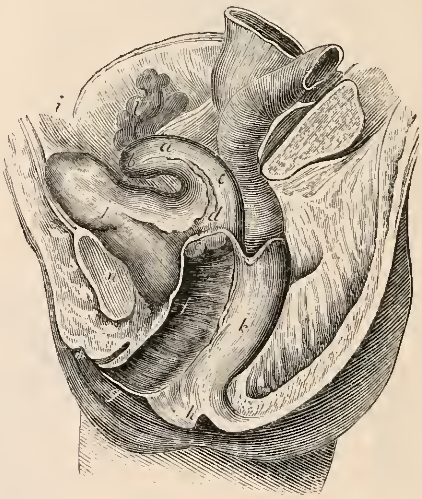
Antiflexion of the uterus. (*After Boivin and Dugès.*)

The point of flexure is at the junction of the body with the cervix. Both canals are laid open. (The figure is viewed from the right side.)

Fig. 466., giving a lateral view of the antiflexed uterus, exhibits the relative situation of its various parts when this deformity exists in the highest degree.

Now a slight amount of antiflexion of the body upon the cervix has been shown by *figs.* 426. and 433. to be natural to the uterus; and it is not until one or two pregnancies have supervened, that this forward tendency, when excessive, is lost, and hardly even then, for the uterus may still retain that correspondence in form, with the curvature forwards of the pelvic cavity, which is so prominently expressed in the curve of the sacrum, and is in accordance with the normal form of the uterine canal. In the fœtus (*fig.* 467.), and during early infancy, antiflexion exists as a

Fig. 467.



Natural state of antiflexion of the uterus in fœtal and infantine life. (*After Bourgery.*)

a, body, and *b*, fundus of the uterus; *c*, point of junction of body and cervix; *d*, cervix; *e*, os tincæ; *f*, vagina; *g*, hymen; *j*, bladder; *k*, rectum; *l*, Fallopian tube; *n*, symphysis pubis; *m*, labium.

normal state, and it appears to me that this bias towards a forward inflexion of the uterus at the early periods of life is given by that remarkable bending forwards of the lower extremity of the spine which is observable in the early embryo. The part containing the structures that are afterwards developed into the uterus exhibits then an abrupt curve, which at this early period will probably be impressed upon the organs within, and being abnormally retained by them after the pelvis has changed its form, may give rise to the malformation under consideration.*

b. Retroflexion exhibits the converse peculiarity, the body of the uterus being bent backwards upon the neck at such an angle that the fundus occupies a position more or less deep between the cervix and rectum, filling and distending the pouch of Douglas. This condition of the uterus ought not to be confounded with retroversion or with those retro-uterine tumours produced by inflammation, and effusion into the cellular tissue (*fig.* 433., G) at the back of the cervix, of which an account will be presently given. See p. 688.

c. Lateral inflexion. — The uterine body exhibits occasionally an inclination to lateral curvature, so that the fundus is directed towards one or other side. A curvature outwards, in the form of an arch more or less deflected from the meridian, has been shown to be the usual condition of the uterus unicornus. But where a tendency towards either side is shown in the otherwise normally formed organ, this appears to arise from some inequality in the development of the two uterine halves; or it may depend upon one half undergoing hypertrophy, so that in either case one uterine angle lies higher than the other, and a vertical line would divide the organ into two unequal parts. The cervix is here curved as well as the body, or the latter may remain perpendicular while the body is bent so as to form an angle with the cervix. The former variety has been designated the retort-shaped uterus.

Anomalies of Position.

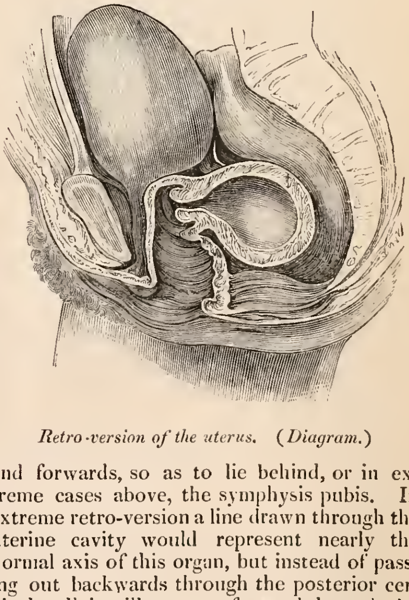
Obliquity of position, Hysteroloxia, Metroloxica, Obliquitas uteri.—The foregoing defects should not be confounded with those deviations in position, without alteration of form, which constitute the various obliquities of the uterus; — like the inflexions of the uterus they are distinguished according as the organ is directed forwards or backwards in the median line, or laterally in the transverse diameter of the pelvis.

a. *Anti- and retro-versions. Situs uteri obliquus anterior et posterior.* — Anti-version of the uterus is by no means so common as retroversion. Both affections differ from the corresponding anti- and retro-flexions of the organ in this respect, that while in the two latter cases the point of flexion is usually at the seat of junction of the body with the cervix uteri, in the former the uterus remains straight or nearly so, while the entire organ is directed forwards or backwards, and the seat of flexion is at the junction of the cervix with the vagina. The displacement of the uterus is here far more considerable than in the former cases.

In *anti-version* the degree of uterine displacement is limited by the bladder and anterior wall of the pelvis, which generally prevent the fundus from sinking so far forwards, as to give the entire uterus in the unimpregnated state more than a horizontal direction. An extreme degree of anti-version however sometimes occurs at an advanced period of pregnancy in multiparæ, on account of an unusual laxity of the abdominal walls permitting the whole uterus to fall forwards, so as to occupy the artificial pouch formed by the pendulous abdomen, the fundus filling the bottom of the pouch, while the cervix and os uteri are tilted upwards and backwards, the latter being lifted out of the pelvis, and pointing above the promontory of the sacrum. This malposition materially impedes labour by reversing the natural direction of the uterine axis, so that the propelling force is expended upon those parts that lie opposite to the os, and the fœtal head is prevented from entering the pelvic brim.

Retro-version occurs in conditions of the uterus otherwise normal, or it may happen when the organ is enlarged by disease or pregnancy. When unimpregnated the displaced organ lies entirely, and when pregnant chiefly, within the pelvic cavity. In retro-version, on account of the excavation of the sacrum, the fundus readily descends so low as to admit of the normal relations of position of the os and fundus being nearly reversed. The latter being directed downwards and backwards towards the coccyx, while the former is tilted upwards

Fig. 468.



Retro-version of the uterus. (*Diagram.*)

and forwards, so as to lie behind, or in extreme cases above, the symphysis pubis. In extreme retro-version a line drawn through the uterine cavity would represent nearly the normal axis of this organ, but instead of passing out backwards through the posterior cervical wall, it will pass out forward through the anterior wall, because the stretching of the vagina in these cases will cause a slight degree of flexion of the cervix downwards. The sequelæ of this displacement in the case of the gravid uterus, when artificial or spon-

* See a paper in the Trans. Micr. Soc. vol. v. pl. 7.; Quarterly Journ. Microscop, Scien., July, 1857, in which I have figured a human embryo of four weeks, exhibiting this peculiarity in a marked degree.

taneous reposition cannot be effected, are usually premature expulsion of the ovum or sloughing of the uterine parietes and slow discharge of the contents by fistulous openings into the vagina, rectum, or other parts.

b. *Hernia of the uterus. Hysterocele, Metrocele.* — This displacement is rare. The uterus may escape from the pelvis by some of the natural openings which ordinarily admit of hernia, or by an aperture artificially formed, as, for example, between the muscular fibres of the abdominal walls. In uterine hernia, the displaced organ is often accompanied by other parts, almost always by its own appendages, and commonly by a portion of intestine, or omentum. Uterine hernia may be congenital or acquired. It may occur to the unimpregnated or the gravid organ, and in the latter case the development of the fœtus may proceed to the full extent while the organ occupies this unusual situation.

A careful examination of the recorded cases of uterine hernia leaves it doubtful if the precise form of the hernia has been, or indeed could be, determined in every instance.

Ventral hernia has been observed only of the gravid uterus, which may become, in part at least, included in a large umbilical hernia, or it may result in cases of separation of the recti muscles where the uterus has ascended sufficiently high to fall forwards over the brim of the pelvis. And it has been supposed to occur after the cicatrisation of a supra-pubic abscess, and as a consequence of a Cæsarian section.

Of *crural hernia* an interesting example is given by Lallemand *, in a woman aged eighty-two, whose body he examined. The hernia appeared at the age of forty, after labour. It remained as an irreducible tumour in the right groin, and was twice accompanied by symptoms of strangulation. After death, the sac of the hernia was found to contain the uterus, ovaries, Fallopian tubes, and upper part of the vagina, together with two folds of omentum.

Inguinal hernia. — Chopart † relates a case of hernia in which the uterus with the Fallopian tube and left ovarium occupied a sac beyond the inguinal ring. The uterus was small, flabby, and elongated. Lallemand ‡ gives a corresponding case where the uterus and right tube and ovary were found in a hernial sac on the right side in a woman who lived to the age of seventy-one.

The most remarkable examples are those in which the uterus either became pregnant while so situated, or was protruded during pregnancy.

In two examples of this kind, related by Sennert, the precise nature and situation of the hernia is, perhaps, doubtful, but they are nevertheless very interesting.

In the first, a swelling in the left groin followed the blow of a stick. Soon the swelling expanded, and it became in time evident that this was caused by the presence of a gravid uterus. The tumour, covered by integument, hung forward like an oblong gourd; by degrees movements of the fœtus were perceived, and the woman having at length reached her term of pregnancy, the integument and uterus were laid open, and the child and placenta extracted.

In Sennert's second case, some injury had been received in the first confinement, but it was not until after the ninth delivery that a swelling appeared in the left groin, and gradually increased to the size of a cow's bladder; finally it hung down to the knees. The tumour was opened, and a living child extracted. Both cases ended fatally to the mothers.

The best authenticated case is one which occurred at Salamanca, and is related by Professor Ladesma. A woman, age 42, mother of seven children, and the subject of an irreducible inguinal hernia, when 3 to 4 months pregnant experienced a sudden increase of the tumour after stooping. The swelling, now of a different consistence, could not be reduced, and after a time fœtal movements were perceptible within it. Labour ensuing in the usual way, the liq. amnii escaped per vaginam, but it was necessary to extract the child by incision into the sac. The tumour contracted ultimately to the size of an ordinary scrotum, and formed a permanent hysterocele in the inguinal ring.*

In addition to these forms of uterine hernia, a partial displacement of the organ through the obturator foramen or ischiatic notch appears possible. This latter is distinguished by the not very appropriate title of *hernia dorsalis* uteri.

Prolapsus.—Falling of the Womb.—Bearing down.—Two degrees of this displacement are recognised. In the first the uterus occupies a situation lower than usual, the cervix resting upon or near the floor of the pelvis, yet without any protrusion of the organ externally. In the second, the uterus is protruded partly or completely through the vulva. The former is distinguished as partial, and the latter as complete prolapsus or procidentia uteri.

Prolapsus in the first degree is not necessarily accompanied by any material change in the condition of the uterus itself. The following alterations, however, in its relations to surrounding parts usually result. The whole organ occupies a lower position than usual in the pelvis. The vagina is more or less completely filled, its upper part becoming folded upon itself like the half inverted finger of a glove. The cervix is abnormally directed forwards. The uterine appendages become in part displaced in following the descent of the uterus, while the neck and posterior wall of the bladder, and sometimes a small portion of the rectum, are likewise drawn down on account of their attachments to the cervix uteri.

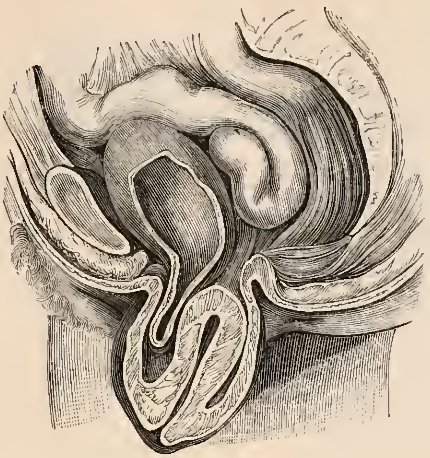
In extreme prolapsus or procidentia, the

* Bulletin de la Fac. de Méd. tom. i. 1816.
† Boyer, Traité des Mal. Chir. t. viii. p. 381.
‡ Mém. Soc. Méd. d'Emulation, 3me Ann. p. 323.

* Edinb. Month. Journ. Pt. vii. 1841.

entire uterus, or a great portion of it, hangs forth beyond the vulva, forming there a pyri-

Fig. 469.



Extreme prolapsus or procidentia uteri. (Diagram.)

form tumour of considerable size. At the bottom of this is the os uteri, greatly exceeding in dimensions in chronic cases the ordinary condition of the part. (*Fig.* 472.) The lips are swollen and hypertrophied, and usually present a sore and granular surface on account of the friction to which they are continually exposed. The external covering of this tumour, in all but its lower part, consists of the inverted vagina, the horizontal rugæ of which are very conspicuous anteriorly between the cervix and pubic arch, where a fluctuating swelling is observed, caused by the presence of a portion of the displaced urinary bladder. (*Fig.* 469.) In chronic cases the surface of the inverted vagina gradually loses the character of a mucous membrane, and puts on the ordinary appearance of common integument. After replacement, however, an extensive shedding of epidermal scales ensues, and the surface resumes in time the condition of a mucous membrane.

In cases of great elongation of the cervix, the latter alone may protrude, while the body of the uterus remains within the pelvis. Such a combination of hypertrophy with displacement has passed with the ignorant for an example of hermaphrodite formation.

Prolapsus is the most common displacement to which the uterus is subject. It is frequent in multiparæ, and in women who follow fatiguing occupations, especially those of a relaxed habit of body; but it also happens in nulliparæ. In the latter, when it occurs at an early period of life, it is often associated with enlargement of the uterus or its appendages, whereby both the weight of the organ is increased, and a broader surface is offered for pressure from above.

Elevatio uteri. Dislocation upwards.—This is the converse displacement to the foregoing. The uterus, in consequence of some enlargement of the parts appended to it, as the ovary, or on account of the formation of morbid adhesions, may be drawn upwards to such an extent that no portion of it, or only a part of the cervix, is retained within the pelvic cavity. This displacement is also occasionally observed during pregnancy, and in multiparæ, whose abdominal walls are relaxed, and permit the uterus to incline forward, so that at the beginning of labour the os cannot be reached by the finger.

Inversion. Eversion. — The uterus, either in the unimpregnated or gravid state, may become partially or completely inverted. The conditions which appear ordinarily to combine in producing this displacement, are, first, a distension of the uterine cavity*, as by pregnancy or the presence of a tumour; and secondly, a force applied in the way of pressure from above, or traction from below, whereby the distended uterine walls become folded within each other, somewhat after the manner of the intestinal walls in intussusception. Inversion of the uterus appears always to begin at the fundus which is first depressed into the uterine cavity, and then, under the continued operation of the disturbing forces, the part is gradually protruded through the cervix and os uteri, *fig.* 470., until it emerges in an inverted form into the vagina followed by the reversed walls of the uterine body, and ultimately by those of the cervix. The inversion of the uterus is now complete. The greater part of the organ lies beyond the vulva as a pyriform tumour, the base of which, formed by the fundus, is below, while above the narrower neck of the tumour consisting of the inverted cervix lies in part within the vagina, the upper portion of which canal is also drawn down and partly inverted. The vagina is thus materially shortened, and terminates in a circular fold marking the point of reflexion or inversion, while the usual seat of the os uteri, which is necessarily obliterated, is occupied by the now inverted cervix (*fig.* 471.).

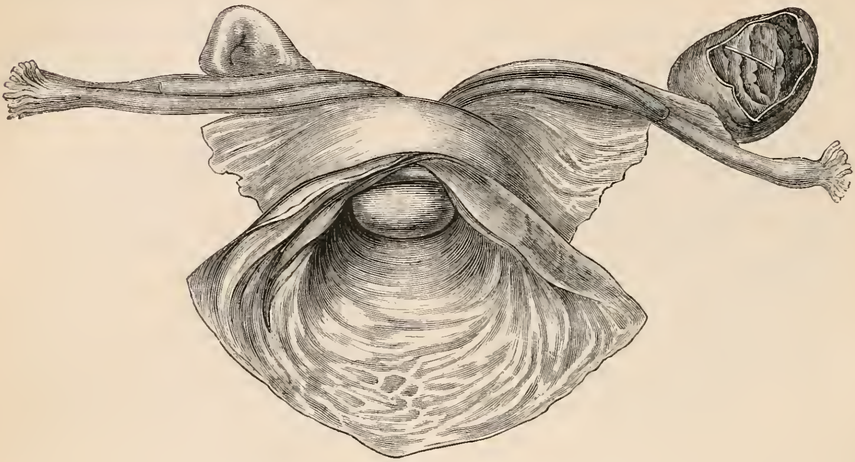
Inversion constitutes the highest degree of displacement of which the uterus is susceptible, for it is both prolapsed and inverted, so that the relative situation of the entire organ to surrounding structures, as well as of all its parts to each other, is completely changed. Inversion does not, however, always proceed to the highest degree, but may stop short at any of the intermediate stages just described.

When inversion occurs to the gravid uterus, the accident usually happens during the efforts of the organ to expel the placenta. In this way, inversion may occur spontaneously, or it may be favoured or produced by injudicious attempts to extract the placenta, or by too much traction applied to the funis. In the unimpregnated uterus, a polypus attached by a stem to the fundus may by its weight slowly produce the same results. That a sudden and spontaneous inversion of the unimpregnated uterus is possible, was proved to

* Boyer, and some others consider that distension of the uterine cavity is not an essential preliminary to inversion.

me in a case which I witnessed of an aged woman whose uterus became completely inverted during a convulsion. In this instance, the only apparent predisposing cause was the

Fig. 470.



Incomplete inversion of the uterus. (*After J. G. Forbes.*)

The fundus is beginning to protrude through the os uteri, dragging after it the Fallopian tubes, which are drawn into the hollow formed by the inverted organ.

dilatation of the uterine cavity by a tumour the size of a flattened apricot, which was expelled at the moment when the uterus came

Fig. 471.

Complete inversion of the uterus. (*Diagram.*)

down completely inverted, — the violent action of the abdominal muscles and diaphragm probably here producing or aiding the eversion.

After complete inversion, the uterus may remain incapable of replacement. Under these circumstances, the external surface of the protruding portion loses much of its original character of a mucous membrane, and becomes covered by a thicker epithelial layer. It continues, however, more vascular than the surface of an ordinary procident uterus, and is especially liable to abrasion and ulceration, from the friction to which it is exposed. When this displacement occurs during menstrual life, and is permanent, the menstrual fluid may be observed at the periods exuding from the surface of the inverted organ.

The internal relations of an inverted uterus depend upon the extent of the inversion. In extreme cases the interior of the tumour consists of a sac lined by the peritoneum, which originally formed the outer covering of the uterus. The centre indeed of the broad ligament may be said to be inverted so as to form a pouch in which are contained the Fallopian tubes and ovaries, and occasionally a portion of small intestine (*fig.* 471.).

In minor degrees of inversion the uterus remains within the vagina, and the peritoneal pouch in its interior contains only the roots of the uterine appendages (*fig.* 470.).

Anomalies of Size.

a. *Atrophy.* — Under this head may be included those examples in which the uterus appears to have been originally well developed, but has since suffered atrophy of its tissues. Such cases are to be distinguished on the one hand from the imperfectly developed and prepubertal forms already described; and on the other from examples of senile atrophy as it occurs in its ordinary course. Whenever atrophy attacks the uterus before the climacteric change the condition is to be deemed abnormal. Such a wasting may affect the entire uterus or some of its parts. In either case the tissues become pale, soft, and nearly bloodless. In atrophy of the uterine body the walls may not exceed in thickness or density those of the urinary bladder. Such a condition may occur under dilatation of the uterine cavity, which however is more commonly attended by an increase in the thickness of the uterine parietes. The atrophy of the uterine walls which is accompanied by dilatation of the cavity, is distinguished as *excentric*, and that which occurs in combination with a diminished cavity as *concentric* atrophy.

Atrophy of the cervix may be combined with partial atresia of its canal, and is often associated with some malposition or morbid growth of the uterine body or its appendages.

b. *Hypertrophy* is of far more frequent occurrence than uterine atrophy. According as this condition affects the entire uterus or only some of its parts, the organ either presents the ordinary figure but upon a larger scale, or else a greater preponderance is given to one portion, so that the uterus becomes malformed. Hypertrophy of the entire uterus commonly results from frequent pregnancy, from the growth of tumours, or from accumulation of fluid within the cavity. In the latter cases the uterine walls may acquire the same thickness as in pregnancy—and the hypertrophy is due also to the same cause, viz. to a development of smooth muscular fibre, such as ordinarily takes place in the gravid uterus.

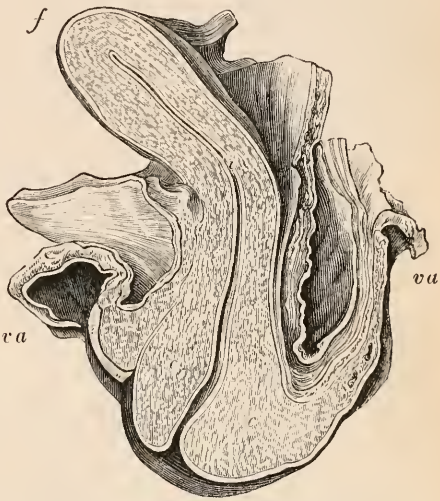
Hypertrophy of the cervix is most frequently observed in extreme prolapsus, of which in the chronic stage it appears to be a constant sequence. Here the hypertrophy produces usually a uniform enlargement of both lips, which form together an annular tumour divided transversely by a wide os tincæ, *fig.* 472.

Fig. 472.

Hypertrophy of the os and cervix in prolapsus uteri. (*Ad Nat.*)

But the cervix may become hypertrophied in the longitudinal direction also. From this there results a remarkable elongation of the uterine neck, which may protrude to a considerable distance beyond the vulva without a corresponding degree of displacement or descent of the body of the uterus. In the accompanying illustration, *fig.* 473, the manner of growth of the elongated cervix is shown. The body of the organ being only partially displaced, a gradual addition to the length of

Fig. 473.



Elongation of the cervix uteri from longitudinal hypertrophy. (*Ad Nat.*)

f, fundus; *i o*, internal os uteri; *c c*, cervix; *v a*, vaginal walls.

the neck occurs until the vaginal portion protrudes at the vulva. The canal of the cervix may now measure several inches in length. By degrees the protruded part undergoes in addition the concentric and excentric hypertrophy which is common to all cases of procidentia, and the lips gradually acquire the same appearance as in *fig.* 472.

Among the anomalies of size may also be included those examples of imperfect involution of the uterus after pregnancy, in which the organ retains for several months the ordinary size characteristic of it shortly after labour.

Pathological conditions of the separate tissues of the uterus.—Reserving for future notice the affections of the gravid uterus, those morbid states which are observed in the unimpregnated organ will be at present considered. These may be divided into such as belong to (1) the peritoneum; (2) the subperitoneal tissue; (3) the parenchyma; and (4) the mucous lining of the uterus.

1. *Pathological conditions of the peritoneal coat.*

a. The external position of the peritoneal coat, and the small amount which it contributes to the bulk of the uterus, combine to render the morbid conditions of this coat, regarded singly, of less pathological importance than the abnormal states of the other tissues. The pathological conditions of the serous coat are chiefly those of *acute or chonic metroperitonitis*, terminating often in exudative processes and the subsequent formation of adhesions between those portions of the uterus which are invested by peritoneum and adjacent structures, such as the Fallopian tubes, ovaries, *fig*. 420., small intestines, and the like.

These adhesions are occasionally so extensive as to affect the figure of the uterus, and in most instances they deprive it of its natural mobility, and impede or destroy the functions of the parts or organs appended to it, so that an abiding sterility frequently results. The ovaries becoming invested by a capsule of false membrane, are tied down and atrophied, while the tubes lose their power of motion or their canals become obliterated.

The uterine peritoneum is sometimes alone affected, while the appendages escape. If the inflammation has not proceeded to the formation of bands of adhesion, there may result only some slight processes of false membrane which remain and fringe the surface of the organ. These little fringes or processes, consisting of delicate folds of membrane, often contain vessels which are easily injected.

The peritoneum suffers considerable distension with correlative hypertrophy in the case of tumours which project from the outer surface of the uterus. These become invariably covered by an extension of the peritoneum, which is especially strong about the base of the peduncle occasionally acquired by such tumours.

2. *Pathological conditions of the sub-peritoneal fibrous tissue.*

a. *Perimetritis. Partial chronic metritis. Peri-uterine phlegmon. Retro-uterine tumours.* — The subperitoneal fibrous tissue which connects the peritoneum with the uterine substance, like the peritoneal coat itself, is subject to inflammation. In those situations where the union of the outer and middle coats of the uterus is very intimate, the distinction between a peritoneal and a subperitoneal inflammation may not be possible, but where this connexion is very loose, and is effected by the interposition of a lax fibrous tissue, inflammation may apparently have an independent seat without affecting at all, or with only a partial inclusion of the uterine parenchyma, and sometimes of its peritoneal investment.

The term "*peri-uterine*" has been employed by some authors*, with a view perhaps of avoiding confusion, though at the cost of a solecism, to distinguish these affections from others commonly termed *perimetrial*. In this article, however, inflammation of the subperitoneal fibrous tissue will be designated *perimetritis*, while inflammation of the peritoneum itself, which some include in the latter term, is distinguished as *metro-peritonitis*.

Perimetritis consists in an acute, or more often a chronic inflammation of the tissue, which loosely attaches the peritoneum forming the base of the broad ligament to the proper substance of the neck and lower portion of the body of the uterus. The relation of the peritoneum and of the loose fibrous tissue surrounding the cervix uteri have been described at page 631., where also attention was called to the peculiar lax tissue of this kind which unites the posterior cervical wall with the portion of peritoneum forming the retro-uterine pouch (*fig*. 433. G.). Here, particularly, this inflammatory affection has its seat, although it occasionally extends around the sides of the cervix, so as partially to encircle that part, or more rarely it may involve only the fibrous tissue connecting the anterior cervical wall with the posterior surface of the bladder (*fig*. 426. *b b*, and *fig*. 433. F.).

The anatomical conditions of these perimetrial inflammations are deep congestion of the vessels, accompanied by serous, and occasionally by sanguineous, and possibly fibrinous infiltration of the loose tissue of this part, which, on account of its extreme laxity, readily admits of a great degree of distension. In this way is rapidly formed a tumour which almost invariably occupies the space between the peritoneum and the posterior wall of the uterus, at the point where the body joins the cervix (retro-uterine tumour).

The recognition of such a tumour or swelling during life, by physical signs, is not difficult. The finger introduced into the vagina, so that its extremity reaches the point of reflexion of the posterior wall of that canal forwards on to the uterine neck, discovers, just above this spot, a hard or semi-elastic projection, which seems to grow out of the cervix just at its point of junction with the body of the uterus. The surface of the tumour towards the rectum, upon which it encroaches, is convex, and is either smooth or irregularly nodulated, while between the tumour and the neck of the uterus is usually perceived a notch more or less deep, and comparable in form to that which separates the body from the neck of an ordinary retort. Hence this condition may easily be mistaken for the retorted uterus, which it closely resembles in many particulars. The surface of the tumour is exquisitely tender, while the adjacent uterine structures are free from tenderness.

The comparative frequency of this affection*, and the constant and severe suffering which result from it, especially in married women, in whom it is usually found, may justify here a brief exposition of the peculiar anatomical condition and relation of parts which appear to me to conduce to its production. From the view of the pelvic viscera given in

* Monat, Observation Médicale (Gazette des Hôpitaux, 1850.) Bernutz et Goupil. Recherches Cliniques sur les Phlegmons péri-utérines. (Archives Générales de Médecine. Mars 1857.)

* I believe that it is often confounded not only with retroflexion, but also with retroversion, fibrous tumour, and hypertrophy of the posterior uterine wall, and that hence the frequency of its occurrence has not been commonly recognised.

(*fig.* 433.) it will be seen, that while the normal cervix projects obliquely into the upper part of the vagina, the fornix or blind extremity of that canal forms the actual termination of the tube, so that this arrangement, while it tends materially to the preservation of the os and cervix uteri from injury during congress, at the same time exposes the cul de sac of the vagina to a certain amount of pressure, which various circumstances, such as relative shortness of the vagina and other obvious conditions, may render injurious. But exactly over this spot lies the mass of lax fibrous tissue in question, the meshes of which become easily infiltrated under inflammation by serous or fibrinous fluids supplied by the vessels, which sections of this region show to be so abundant in the neighbourhood. (*Fig.* 429.)

Perimetrial inflammation occasionally reaches the suppurative stage, and in this way are formed some of those abscesses which burst through the cervix, or form collections of matter between the folds of the broad ligament.

3. *Pathological conditions of the muscular or proper coat.*

a. *Diminished and increased consistence* of the uterine substance, although generally resulting from obvious morbid processes, is yet sometimes found without any apparent disease of the tissue.

Diminished consistence may be found in various degrees, from a slight friability or softness to a nearly complete pulpiness (*marciditas*). In these cases the texture of the uterus may be pale and exsanguine, or in a state of hyperæmia, with occasionally apoplectic effusion. Rokitansky associates the latter condition with thickening, and sometimes ossification of the uterine arteries.

b. *Parenchymatous inflammation of the uterus. Metritis. Metritis parenchymatosa.*—Inflammation of the substance of the uterus, which in the puerperal state is so commonly fatal, seldom leads to death in the unimpregnated. Hence opportunities for investigating the anatomical condition of the organ in the non-gravid state under conditions of inflammation are of comparatively rare occurrence. From such opportunities, however, aided by what may be observed during life, the following may be concluded as to the changes which inflammation produces in the muscular and fibrous coat.

Under acute parenchymatous inflammation the whole organ becomes increased in bulk, and at the same time redder and softer. On section blood flows freely from the divided vessels, and the tissues are found permeated by serous infiltration. Sometimes the highly congested vessels have in parts given way, and ecchymoses or larger apoplectic collections have resulted.

If no commensurate resorption of these effusions takes place the organ continues of abnormal size. This is more particularly observable when a portion of the uterus, as the body or cervix, has been repeatedly inflamed. The latter, especially, remains enlarged. The os tincæ is patulous, and one or both lips of the cervix present an œdematous hardness, and occupy a larger space than usual in the fornix of the vagina.

Occasionally inflammation of the uterine parenchyma reaches the suppurative stage, resulting in collections of matter which may escape into the peritoneum between the folds of the broad ligament, or externally by the vagina or rectum.

Chronic inflammation produces likewise a general enlargement of the uterus, but more commonly the cervix is principally or exclusively involved, and the resulting enlargement is especially observable in its vaginal portion, the lips of which become increased in breadth, or elongated and prominent.

When chronic inflammation affects, on the other hand, the parenchyma of the body of the uterus chiefly, the walls of this part become thickened and indurated, while the cavity undergoes enlargement such as is exhibited by the ventricles in excentric hypertrophy of the heart. Under chronic inflammation the uterine tissue becomes indurated, so that upon section it grates beneath the knife. This induration is occasioned chiefly by hypertrophy of the fibrous element of this coat of the uterus.

c. *Fibroid. Tumor fibrosus uteri. Fibro-muscular tumour. Hard fleshy tubercle of the uterus* (Baillie).—These and numerous other titles have been employed by different authors to designate a form of degeneration of the uterine tissue which is so common that, according to the often quoted calculations of Bayle, it may be found in every fifth case of women who die after the age of thirty-five.*

Fibroid of the uterus has for its basis the same structure as fibrous tumours in general.† The surface of a section presents to the naked eye a peculiar mottled appearance, caused by the presence of numerous white lustrous bands intersecting in all directions a more homogeneous basis substance, which in these uterine formations has always a greyish or light brown colour, the latter being especially distinct in spirit preparations. The difference between these two, however, is more apparent than real, consisting, as Paget suggests, rather in the mode of arrangement than in an actual differentiation of the component structures. These consist chiefly of very slender filaments of fibrous tissue "undulating or crooked," and exhibiting various degrees of development in different specimens, being in some large and wavy, and in others very short, and often intermixed with cytoblasts and nuclei. Along with this fibrous basis is found a variable amount of smooth muscular fibre, which in some cases, especially in the polypi hereafter noticed, forms the chief bulk of the

* Dr. West has furnished some interesting statistics upon this subject. (Lectures on the Diseases of Women, Pt. i. p. 277. 1856.)

† For an account of these see Paget's Surgical Pathology, Vol. II. Lect. V.; and also for those of the uterus, Bidder, in Walter ueber firbröse Körper der Gebärmutter.

mass, so that a muscular rather than a fibrous tissue results. A small quantity of elastic fibre is also occasionally found in these uterine formations.

Fig. 474.

Section of fibroid tumour of the uterus. (*Ad Nat.*)

The structural variations observable in fibroid of the uterus, are dependent chiefly upon the peculiarities in arrangement of these component elements. In the more dense formations, the white shining fibrous bands enclosing little pellets of the browner substance, form numerous small compact masses, which are again closely united together by a somewhat looser fibrous tissue that serves to combine the whole into lobes or lobules, varying in size from a pea to that of a man's head. The variation in density of these masses depends, further, upon their vascularity. In the softer kinds, bloodvessels that may be injected permeate the mass, running along the bands and layers of fibrous tissue connecting the lobules. Such tumours are sometimes of a deep red colour. The denser masses, on the other hand, are apparently nearly bloodless; at least, injections cannot be made to penetrate them.

The different configurations which these masses of uterine fibroid assume, appear to depend in a great measure upon accidental conditions. In this particular three varieties may be noticed.

1*st var.* *Interstitial fibroid.* — The mass here forms a growth, sometimes of immense size, but still contained within the proper boundaries of the organ, occupying one or other uterine wall, but neither encroaching upon the uterine cavity, nor protruding externally. Such is the case represented in *fig.* 475., in which the external appearances were those of the ordinary gravid uterus in the seventh month. Such masses appear occasionally at their periphery to merge gradually into the healthy tissues of the uterus, but more commonly there exists a distinct boundary formed by loose cellular tissue with which the tumour is so lightly connected that it may be easily detached and turned out of its investing capsule (*fig.* 475).

Fig. 475.

Interstitial fibroid of the uterus. (*Ad Nat.*)

The tumour is formed in the substance of the posterior wall, which is so attenuated at one spot as to be nearly broken through. The cavity of the uterus is shown in the lower part of the figure unaltered in size.

2*nd var.* *Subperitoneal fibroid.* — In this variety the fibroid mass or masses protrude from the external surface of the uterus. Here one or several round or oval tumours are formed which seem to grow out of the uterine substance by a narrower or broader base, or they remain attached to it by a peduncle. These masses consist entirely of fibroid, having either simply an investment of peritoneum, or beneath that also, in many instances, a layer more or less thick of uterine substance which is usually laminated, so that a capsule composed of the natural tissues of the uterus is formed around the tumour (*fig.* 476.).

3*rd var.* *Sub-mucous fibroid.*—In this variety the fibroid mass quits its bed in the uterine walls, and projects into the cavity of the uterus; it becomes covered by an extension of the lining membrane of the uterus, and sometimes also beneath this by a layer of healthy uterine tissue. These tumours, when they possess a peduncle, constitute the fibroid polypi of the uterus.

A distinction has been made in these polypi between such as form continuous outgrowths from the substance of the uterus, and those in which the polypous mass forms a discontinuous tumour, connected only by a narrow stem of mucous and muscular tissue.

The original position of the fibroid growth in the uterine walls, whether in the middle or nearer to their inner or outer surfaces, probably determines, in a great measure, the direction and form which these growths ultimately take, and is consequently productive of the three varieties above noted.

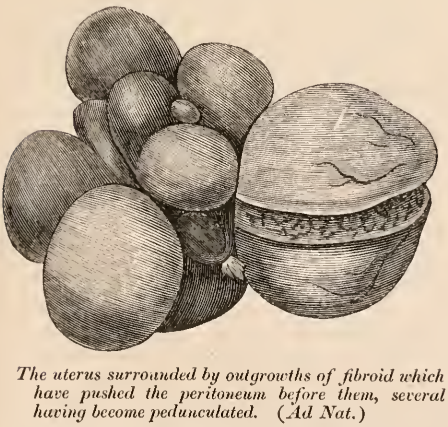
The different forms which fibroid assumes are in accordance with these varieties of position. Fibroid growths retained within the uterine walls, are at first almost invariably spherical, but in course of growth become ovate or flattened. Those which project from the outer surface are usually nearly round, while the polypi of the cavity, and those which extend into the vagina, are pyriform, and possess longer or shorter peduncles. The greater part proceed from the fundus, comparatively few from the walls of the body, and scarcely any of this kind from the cervix. The latter are usually of a more spongy or cellular character than the former, which consist of a denser fibrous tissue.

The power of growth of fibroid tumours appears to be nearly unlimited. The known extremes in such cases are, in point of number, from one to forty; and in respect of weight, from a few grains to seventy pounds.

Fibroid exercises a considerable influence upon the form and position of the uterus. Tumours within, or external to it, change the position of the organ in various ways, producing elevation, prolapsus, lateral obliquity, and especially retroversion, according to the seat which they occupy. Polypi distend the cavity of the body and cervix, and the os uteri, and sometimes produce prolapsus and inversion of the uterus.

The influence of fibroid upon the thickness of the uterine walls is also considerable. Generally a marked hypertrophy, equal sometimes to that of pregnancy, takes place, while in parts a thinning of the walls occurs. The latter is especially observable in cases where the tumours are numerous, as in *fig.* 476. These sometimes appear to grow at the expense of the whole uterine substance, so that the original organ is with difficulty discovered among the hypertrophied mass.

Fig. 476.



The uterus surrounded by outgrowths of fibroid which have pushed the peritoneum before them, several having become pedunculated. (*Ad Nat.*)

The uterus, at the expense of whose tissues the tumours are formed, can scarcely be discovered in the midst of the mass.

Important consecutive changes take place during the process of growth of fibroid. So long as the structure retains its original hardness, the increase is comparatively slow, consisting in a simple and uniform multiplication of the elements already described. Occasionally an increase of density is produced by calcification of certain portions of the mass, and in this way the so-called bony tumours of the uterus are formed. Or, on the other hand, under rapid growth, the tumour may become softer, in consequence of serous infiltration into its tissues; the fluid occasionally collecting in the centre of the tumour and forming there a species of dropsy. Or, a process of inflammation being set up, suppuration, and sometimes sloughing, result. In the more vascular fibroids the vessels may dilate and burst, and the tumour then becomes infiltrated with extravasated blood. It has been doubted whether fibroid ever undergoes absorption. I have reason to think, from occasionally witnessing a marked diminution in bulk, that this may sometimes occur. The explanation of this is indeed easy when the mass of the tumour consists of hypertrophied muscular tissue, which in such cases has been found to undergo fatty degeneration, and so its dispersion may be effected.

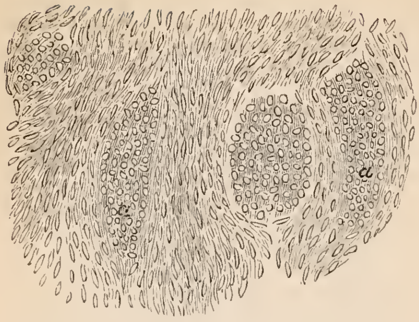
Subperitoneal and interstitial fibroid, when extensive, interferes with pregnancy, and also renders labour difficult or perilous, by weakening the expulsive power of the uterus and predisposing the organ to rupture. Submucous fibroid, in the form of polypi, may prevent impregnation or shorten gestation. In the unimpregnated uterus, all forms, but especially the submucous and interstitial, are apt to be accompanied by severe recurrent hæmorrhage, producing excessive anæmia and occasionally death.

Lastly, it may be observed, in reference to tumours which are commonly termed polypi, that the present state of pathology demands a separation of these, according to their structural differences, such as has long been established, upon a similar basis, among those objects of the animal kingdom whose supposed resemblance, distant indeed, and at the best fanciful, has given a name to this form of tumour. For, as in that prototypal group of animal forms, once termed polypi, three widely separated classes at least are now known to have been combined, so those pathological formations, which are still familiarly termed polypi, exhibit a more than equal number of varieties, each marked by distinct differences of structure. These may be distinguished as the *fibrous*, including the cellular, which are composed of a looser fibrous tissue; the *muscular;* the *mucous*, also frequently containing much fibrous tissue, and the *cancerous* or *malignant* polypi. And to these have been added the so-called *fibrinous* or *blood* polypi.

The fibrous polypus has been already described, and the second, or muscular, may here also be classed with it, as having its origin in the middle coat of the uterus, but consisting of muscular rather than of fibrous tissue.

These muscular polypi are comparatively rare. Their structure, as exhibited in the accompanying *fig.* 477., is precisely that of the proper muscular coat of the uterus.

Fig. 477.



Section of a polypus formed of the muscular tissue of the uterus. (After Wedl.)

The fibres, arranged in bundles, run in different directions. At *a a*, they have been divided transversely, and in other parts obliquely. Compare with *fig.* 436.

The malignant polypi, and those which are formed of hypertrophied mucous structure, belong to another category, and will be described hereafter.

4. *Pathological conditions of the mucous coat.* — *a.* First under this head may be noticed *simple hypertrophy* of the uterine mucous membrane, followed often by a partial shedding of that structure in the form of the so-called

Dysmenorrhœal membrane.—The term *menstrual decidua* would probably form a more appropriate title for these structures, which consist of a greater or less thickness of the mucous membrane lining the uterus, differing in no respect from that membrane in its ordinary condition *, except in the one particular, that it has undergone a certain degree of hypertrophy. (*Fig.* 443.) The hypertrophies which the mucous membrane of the uterus undergoes in various circumstances form a most interesting subject for study, but all of them are not pathological. The most familiar example of normal hypertrophy of the uterine mucous membrane is that which occurs in ordinary pregnancy. Here, no sooner does the uterus begin to enlarge, than the mucous lining also expands, and its tissues become opened up by an increased flow of blood, and a consequent rapid development of the simple elements composing this structure. This hypertrophy occurs in every pregnancy where the ovum enters the uterus. But it also happens very generally in those cases where the ovum never enters the uterus at all, but is developed externally to that cavity (extra-uterine gestation). Here a most perfect decidua is usually found lining the uterus. The exceptions are few in which the uterine mucous membrane, under these circumstances, does not exhibit any increase of thickness, but retains or nearly so, its ordinary characters

* See on the structure of the uterine mucous membrane, p. 635. of this article.

But a state of pregnancy is not necessary to produce evolution of the uterine lining, for this may occur when the body of the uterus is enlarged from other causes. Thus, in an example in my possession of uterine fibroid, in which the body of the uterus has undergone the hypertrophy already described (p. 491.), as common in that state, the hypertrophy has extended to the mucous membrane, so that the uterine cavity, which had also been occupied by one of these tumours, exhibits a delicate decidual lining.

The decidual membranes occasionally cast off from the uterus under circumstances of dysmenorrhœa, consist of fragments, or, more rarely, of entire membranes forming casts of the uterine cavity. The structure of all these is nearly similar, and they differ chiefly in the greater or less thickness of membrane detached. All present upon their inner surface the peculiar cribriform markings already described as constituting the orifices of the uterine glands, while their outer surfaces are rough and shaggy, like the outer surface of aborted ova, for this surface has been detached or torn off from the uterus. *Fig.* 443. represents a portion of such a membrane, as seen from its inner or cribriform surface. The microscopic characters of these membranes are precisely those of ordinary decidua.

b. Hypertrophy of the follicular structures of the uterine mucous membrane. Follicular polypi. Mucous polypi. Cysts. — The pathological formations which take their origin in the mucous membrane lining the uterus, consist chiefly in hypertrophic growths of that membrane, and of its follicular structures. They present usually two varieties, according as the follicular or the ordinary mucous tissue abounds in their composition. Many of these growths acquire a peduncle, and then constitute the mucous or follicular polypi.

The follicular structure is most apparent in those growths which spring from the body, and especially from the fundus uteri near the orifices of the Fallopian tubes. These vary in size from a pea to a small plum. They have usually a rounded or oval form, and become partially flattened by the external pressure of the uterine walls. A short and narrow peduncle connects them with the spot from which they arise. Externally they are smooth and covered by a layer of epithelium, beneath which is a thin extension of the uterine mucous membrane. This is often sufficiently transparent to render visible numerous opaline spots, indicating the seat of groups of uterine follicles distended and elongated, and containing a semitransparent gelatinous fluid. Between these elongated follicles there is a loose fibrous tissue connecting them together, and giving substance to the mass. These tumours possess little resistance, and are usually soft and elastic.

The more solid mucous tumours very generally acquire a stem, and early take the form of polypi. These mostly arise from between the folds of the lining membrane of the cervix, and are evidently mere hypertrophies of that structure, including a variable proportion of the sublying cervical fibrous tissue. In size they range from a pea to a walnut, and occasionally their peduncle measures several inches in length, so that they may pro-

Fig. 478.

Pedunculated polypus of the cervix uteri. (*After Boivin and Dugès.*)

trude to a considerable distance beyond the vulva. Their form is generally that of an elongated pear. The surface is smooth, though not uniform, being usually nodulated or lobed, and in parts roughened by minute papillary growths. Sometimes one or two of the cervical folds or rugæ, scarcely altered in character from their ordinary condition in the healthy cervix, are distinctly visible upon them. These more solid tumours are covered by cylinder or pavement epithelium and hypertrophied mucous membrane. Internally they are composed of loose inelastic fibrous tissue, containing a few enlarged and obstructed follicles, one or two of which may grow more than the rest, and form a cavity distended by a slimy fluid.

The growth of both these forms appears to be limited, and they never attain to the size which the fibrous polypi often reach. With the hypertrophies of the follicular structures are also to be classed those single cysts, of the size of a pea, or larger, and sometimes pedunculated, which are very commonly found lying between the cervical folds, or protruding from the os uteri. These consist almost exclusively of distended Nabothian follicles.

c. Hypertrophy of the filiform papillæ of the cervix. — A variety in the condition of the filiform papillæ upon the vaginal portion of the cervix has been described at p. 639. These papillæ, nstead of being short, and covered by pavement epithelium up to the very margin of the os uteri, as they are upon the rest of the cervical lips, may present the same condition which they have within the cervix, where they are longer and larger, and are not bound down by a continuous layer of covering epithelium. These papillæ often appear at the margin of the os, and form there little tufts, or extend over the lips of the cervix in the crescentic manner already described at p. 639. They then constitute one of those conditions to which, in the present day, the term ulceration is very frequently applied; yet there is no more reason for asserting that these are pathological formations or conditions, than there is for asserting the same of the villi within the canal, for both are identical in form. They can only be regarded as pathological structures when they obviously exceed the natural conditions already described. Then, indeed, they may be classed among the hypertrophies of special structures of the cervix, and they will bear the same relation to the natural papillæ, that the hypertrophied follicular structures, forming the cysts and polypi recently described, bear to the cervical follicles in a healthy condition. Both the hypertrophied and the natural papillæ give to the finger that peculiar velvety or mossy sensation which is usually classed among the diagnostic signs of ulceration of the os uteri.

d. Simple inflammatory hypertrophy, with extroversion of the cervical mucous membrane. — The mucous membrane lining the canal of the cervix uteri under chronic inflammation becomes frequently partly everted, so that a portion of the inner surface of one or both walls of the neck is rendered visible at the lower orifice, taking here the place ordinarily occupied by the inner border of the lips of the os tincæ. This affection is usually combined with a corresponding hypertrophy of the proper tissue of the cervix, and may be compared in its effects to that thickening of the upper lip common in strumous children, which causes the part to become everted.

Figures 7. and 8. Plate IX. in Boivin and Dugès' Atlas represent an extreme degree of this affection, in which the cervical mucous membrane protrudes to an unusual extent, so that the palmæ plicatæ and middle raphé on both sides are seen. In the more common minor degree of hypertrophy with eversion, a crescentic protrusion only of the cervical mucous lining occurs. The unevenness of the surface, caused by the slightly swollen and prominent rugæ, and as often by the numerous little depressions consisting of enlarged mucous crypts, according as one or the other of these is the predominant normal structure in the cervix *, gives to the part during life the appearance of a raw or granular surface, while

* For a description of these varieties, see p. 640.

the natural boundary between the lower edges of the cervical canal and the lips of the os tincæ being now transferred on to the latter in consequence of this eversion, an abrupt semicircular line becomes visible, which, while it only indicates the natural termination here of the vaginal epithelium (see p. 640.), is frequently mistaken for the margin of an ulcer.

This condition may be observed upon only one lip, or upon both simultaneously. It requires special notice here, not so much for its pathological importance, which appears to me to have been overrated, as on account of certain views of late connected with it, under the belief that it constitutes another form of ulcer of the os or cervix uteri.

c. *Catarrhal inflammation of the mucous coat. Endo-metritis. Metritis catarrhalis. Metrorrhœa. Catarrhus uteri. Acute and chronic catarrh. Leucorrhea. Fluor albus.*

The ordinary inflammatory affections of the uterine mucous membrane in the unimpregnated state, which were formerly known only by the discharges to which they give rise, and which were consequently confounded with similar affections of the vagina, have in recent times been more accurately examined, and traced to their real seat. That the lining membrane of the uterus, and its cervix in a state of acute or chronic inflammation, is the principal source of many of these discharges, is now well ascertained, and the similarity of these affections to the catarrhs of other mucous surfaces is now also generally admitted. Hence the term uterine catarrh, under the various forms above quoted, has been employed in most recent works on uterine pathology to designate these affections. Inflammation, whether acute or chronic, may involve the entire uterine mucous membrane, or it may be limited to that of the body or cervix.* The ordinary anatomical conditions of this membrane under inflammation are, first, deep hyperæmic congestion, so that the surface presents a uniform florid red colour, or it is mottled with patches of red, intermixed with paler and less vascular parts. In congestion of the mucous membrane lining the body of the uterus, the superficial capillaries, whose healthy forms are represented in *figs.* 439 *a* and *b*, become intensely loaded, so that rupture occasionally takes place, followed by effusions into the substance of the membrane. A serous or sero-sanguinolent, and in more advanced stages, a muco-purulent fluid, covers the surface, while the entire mucous membrane becomes swollen, softened, and infiltrated with serum. An abrupt line of demarcation, when the congestion is limited to the uterine body, marks the boundary between that cavity and the cervix, the lining membrane of which may retain its natural pale colour,—just such an abrupt line of demarcation between the highly congested membrane of the uterine body and the paler lining of the cervix, as occurs during menstruation or in early pregnancy.*

When inflammation affects chiefly or exclusively the cervical mucous membrane, this becomes turgid and swollen, and its vessels congested. The congestion affects more particularly the capillaries of the vaginal portion of the cervix, and of the interior of the canal near the orifice. The lips of the os tincæ are at the same time tumid, the os is enlarged, and the cervical canal expanded; changes which indicate that the structures immediately beneath the mucous membrane are then also involved. A loss of epithelium in the neighbourhood of the external orifice, more or less extensive, may occasionally accompany the severer forms of this affection. From this it results that the turgid and vascular papillæ beneath becomes exposed, and when these are also hypertrophied, the surface acquires the condition commonly termed granular.

The natural or healthy secretions of the cervix become materially altered under catarrh. In a normal state the cervical secretion is sufficient in quantity to cover the mucous folds, and to fill the crypts and furrows, and occasionally to block up the entire canal. It consists of a viscid, tenacious, and nearly transparent fluid, enveloping numerous mucous corpuscles, granules, and epithelial scales.

When the catarrhal state ensues, this fluid is greatly increased in quantity, and, according to the severity of the affection, it passes through the various conditions of a viscid transparent jelly, resembling clear starch or white of egg, of a thicker cream-like fluid, or of a puriform mucus, in colour nearly resembling pus. Blood also is occasionally found mixed with these secretions.†

The ordinary secretions of the cervix, as shown by Dr. Whitehead, have an alkaline reaction within that canal, but they speedily become acid when mixed with the vaginal secretions, which also cause the previously transparent cervical products to become opaque as they pass through the vagina.

Acute specific catarrh of the vagina (gonorrhœa), as well as simple catarrh of that canal, may be associated with the foregoing affections.

Ulceration of the mucous coat. Metro-helcosis. Granular ulcer. Simple erosion, abrasion and excoriation.—These terms have been severally employed to designate certain conditions of the os and cervix uteri, regarding the nature, frequency and pathological importance of which, as is very well known, great diversities of opinion are in the present day entertained.

The affections of the cervix uteri, which

* This distinction, not usually observed by continental authors, has been emphatically made by Dr. H. Bennet. A Practical Treatise on Inflammation of the Uterus. 3d edit. 1853.

* This point, under both these conditions, is illustrated with great fidelity in the coloured delineations of Boivin and Dugès. See Atlas, Pl. I. fig. 4., and Pl. II. fig. 6.

† A descriptive account of some of these fluids, accompanied by illustrations, will be found in the paper of Dr. Tyler Smith, in Vol. XXXV. of the Med. Chir. Trans.

are commonly deemed ulcerative, are admitted by those who so describe them to possess certain characteristic and exceptional features by which they are distinguished from ulcers of other parts. For it is truly asserted, that "whatever the character of an inflammatory ulceration of the cervix the ulcerated surface is never excavated; it is always on a level with, or above the non-ulcerated tissues that limit it, and its margin never presents an abrupt induration."*

Further, with regard to the position of these "sores," two principal circumstances have been almost invariably noticed. As seen by the aid of the speculum, they either present the appearance of a red and apparently raw surface commencing, within the cervix, or at the margin of the os tincæ, and spreading outwardly to a limited extent over one or both lips; or they form numerous isolated red spots, or sometimes depressions dotted at nearly regular intervals over the whole surface of the vaginal portion of the cervix, and varying in size from a pin's head to a millet seed.

It will aid description to take advantage of these peculiarities for the purpose of arranging in two groups or classes the various pathological and other states of the uterine cervix, which severally exhibit the characters just mentioned. Many of these, however, when minutely examined, and tested by the aid of the microscope, so little fulfil the conditions of true ulceration, as to make it appear that such a term could only have been applied to them under, in some instances perhaps a misapprehended, and in others a strained, view of their real nature.

In the first class may be included those cases in which the filiform papillæ of the cervix are in an uncovered state, and either of their natural size or hypertrophied; eversions of the cervical mucous membrane; and hypertrophic growths of the same. All, or nearly all the non-excavated ulcers, so termed, are referable to one or other of these conditions.

Beginning with the normal variety of structure already described, in which the central columnar folds of the cervical mucous membrane take a perpendicular direction (*fig.* 424.), and after running down to the very margin of the os tincæ terminate there in a narrow border, or tuft of filiform papillæ, the simplest form which has been viewed as abrasion, excoriation, or ulcer, is thus produced. The velvety pile, constituting one of the most common features of pseudo-ulcer, being formed by these slightly prominent papillæ, fringing the margins of the os.

In a more marked degree of the same condition, instead of a narrow line or margin, a broader crescentic patch of uncovered filiform papillæ extends outwardly over either or both lips. The papillæ are gathered into little groups, whose appearance, when magnified by a common hand lens, may be compared to miniature wheat-sheaves heaped together. Each papilla is perfectly free and possesses its own proper epithelial coat.* This little group, which may cover half the circumference of the cervical lip, is encircled or semi-encircled by a thin non-elevated margin, where the ordinary pavement epithelium covering the rest of the cervical lip terminates. There is no appearance of any loss of tissue here, beyond that occasioned by the absence of a portion of that dense layer of epithelium, which, like a sheet cast over the papillæ, usually invests them, as far as the inner borders of the cervical lips, with one common covering, in addition to their own proper coat.

These papillæ may retain their normal size, or they may be hypertrophied. On account of the large number of capillaries which they contain, and from the circumstance that they are uninvested by vaginal epithelium, they present a florid and often turgid aspect.

When such a part is brushed over with nitrate of silver, a line of demarcation is instantly produced, the mucus entangled among the naked villi is coagulated, and a cloud of white chloride of silver is precipitated among them, while the parts adjacent which are covered by pavement epithelium are less affected, and exhibit only a pinkish white opalescence, that contrasts with the dead white within, and with the abruptly marked border of the epithelial edge. In this way is produced another effect commonly quoted as a test of ulceration.†

Those bolder and more marked projections of a florid red colour which begin also from the inner margins of the os, and spread outwardly, looking like granulations, consist of hypertrophies of pre-existing structures intermixed occasionally, though more rarely, I believe, with pathological new formations.

Such hypertrophies are chiefly the following, viz. eversion of the cervical lining as described at p. 693.; hypertrophies of the crested folds of that membrane, which when everted, enlarged, and inflamed, constitute the condition termed "cockscomb granulation;" and lastly, distended and closed muciparous follicles gathered in groups around the os and intermixed with the hypertrophied structures just noticed. These latter add to the irregularities and nodosities of the surface, and together with fissures formed by deepened natural folds, and varicose distensions of vessels, constitute the more irregular forms of hypertrophies which have been termed ulcers.

The second class of pseudo-ulcers termed commonly aphthæ and granulations, viz. those which are dotted at regular intervals over the lips of the cervix, but are often more enduring than herpes, and do not usually in their progress coalesce as herpetic spots when contiguous almost invariably do; these consist of

* J. H. Bennet, *loc. cit.* p. 79.

* Regarding the nature of this coat see p. 639.

† Precisely such an effect may be produced upon mucus scraped with a piece of glass from the tongue, and touched with argenti nitras.

enlarged muciparous follicles*, which in three different conditions or stages correspond with three varieties of pseudo-ulcers of the aphthous kind. In the first variety the follicles are closed and project like millet seeds above the general level of the cervix. They contain a little glairy fluid, and may be compared to the distended closed follicles described at p. 640., as occurring within the cervical and uterine cavities. They are almost always placed at such regular intervals apart, that they must be regarded as natural structures enlarged, rather than as pathological new formations.

The second variety consists not of closed but open follicles similarly arranged. Within and at the bottom of many of these may be seen the filiform papillæ enclosed, cup-like, and resembling the stamens in a half opened flower. Similar follicles to these occur sometimes within the cervix under ordinary circumstances.

When these papillæ become hypertrophied and sprout out above the cup-like level of the containing follicles they form florid-looking and elevated spots resembling granulations in appearance, and these constitute a third variety — the "granulations simples sans ulcerations" of Pichard.†

The foregoing examples have been here passed in review for the purpose of illustrating the principal anatomical and pathological conditions of the uterine cervix, which when viewed by the speculum during life exhibit appearances that are regarded by many observers in the present day as affording unmistakeable characteristics of ulceration. With this object they have been here grouped together, but they do not form a class; many of them indeed have no pathological relationship, and to few can the term ulceration be regarded as appropriate. In order, therefore, to eliminate from the category those conditions which have no title to be considered as ulcers, it is needful to apply to them the test of a definition. With this view, and also for the purpose of avoiding the confusion which from the time of Hunter downwards has attended the employment of various terms for the designation of ulcerative processes, of those at least by which the particles of open or exposed surfaces are removed, it may be well to adopt some such distinction as that proposed by Mr. Paget, namely, to regard as abrasions or excoriations those conditions in which the epithelium or epidermis of an inflamed part is alone removed, and those only as ulcerations in which the removal extends further to the vascular or proper tissues beneath the epidermis.‡

Judged by this test, there may be excluded, first, all those apparent sores which, beginning invariably from within the margins of the os, and appearing to spread outwardly more or less over the cervical lips, present a florid and often granular aspect, and being on a level with surrounding parts, and without definite edges or raised border, fulfil all the conditions commonly assigned to ulcers of the uterine neck. These, almost without exception, consist of the inflammatory conditions already described as hypertrophies and eversions of the cervical mucous membrane. The apparently raw surface exposed to the eye is not usually any portion of the outer cervix, but the swollen inner surface of the walls of the cervical canal now everted and brought into view, just as the interior of the lip is brought into view in common strumous thickening about the mouth. The margin of this apparent ulcer is the normal boundary of the os, or line of demarcation between the vaginal and cervical mucous membrane, now disturbed and thrown out of its natural place. The granulations upon this surface are the thickened and inflamed papillæ, follicles, and rugæ of the cervical canal. The edges are not raised because they simply form the boundary between the vaginal and cervical epithelium, and the centre is not depressed, because there is no erosion nor any loss of tissue.

These conditions of the uterine cervix in respect of their true pathological relations are exactly allied, in their different degrees, to the inflammatory conditions of the eyelid termed respectively Lippitudo, Ectropion and granular lid. Both are attended by like hypertrophies of structure and corresponding depravements of their healthy secretions. Both are reduced to their normal condition by similar or even identical methods of treatment, and both are alike entirely removed from the category of ulcers.

Next to these may be enumerated the conditions of the uterine neck which are distinguished by loss instead of hypertrophy of tissue. When this loss consists solely in detachment of epithelium the term "epithelial exfoliation" appears to be a more appropriate designation and preferable in many respects to "excoriation or abrasion," — terms which seem to imply something of violence in the mode of production of these conditions.

Exfoliation of the tesselated epithelium covering the vaginal portion of the cervix appears to take place under some circumstances with great ease. In uterine catarrh for example, this shedding of epithelium commences at the borders of the os, and extends outwardly. Or it may involve the entire epithelium of the vaginal portion of the cervix together even with that of the vagina itself, these being sometimes thrown off like a cast. In such cases, a fresh epithelium is formed beneath the old one that has been detached.*

But if the epithelium is not renewed the villi remain denuded. This condition may be precisely imitated after death by macerating the part for a few days, and then peeling off

* See p. 640.

† Excellent representations of the varieties described above will be found in Boivin and Dugès' Atlas, pl. 25. 27. and 33., and in Pichard, Mal. des Femmes, pl. 3.

‡ Surgical Pathology, vol. i. p. 419.

* See also page 707. and note.

the epithelial covering. And it is probable that profuse discharges lying in constant contact with these parts during life may similarly assist in softening and detaching this structure. But it is deserving of consideration that the papillæ of the outer surface of the os by this uncovering are merely reduced to the same anatomical condition as those of like form within the cervical canal. Whether this deprivation of a natural covering usually found here renders the villi of the outer cervix, which are probably specially sentient structures, more susceptible of irritation, particularly when in a hypertrophied state, is a matter for consideration that would extend the present inquiry beyond its proper limits here. But it is probable that in this way may be explained those constitutional and local erethisms which often accompany faulty states of the uterine cervix; and which have led to such conditions being invested with a degree of importance often in excess of their true pathological value.

But the villi may be found in some specimens denuded of vaginal epithelium, yet without any evidence of inflammatory or other changes. Such a part may appear quite natural. The villi upon the cervical lips, and those within the canal being in every respect identical and alike natural in appearance, so that the strictest microscopical investigation may fail to detect any difference between them. The examination of such specimens has satisfied me that the vaginal epithelium does not always normally terminate precisely at the inner borders of the uterine lips, but may cease at some point short of this.*

In the third place are to be noticed those cases in which the process of removal extends to tissues deeper than the epithelium, *i. e.* to the villi, the vascular and fibrous, and other tissues. The removal of such tissues here necessarily produces excavation with definite borders, and all the characters of a true ulceration. Ulcers of the uterine cervix exhibiting these features are almost exclusively either syphilitic, phagedenic, cancerous, or cancroid, and such as occur upon the surface of a prolapsed uterus. They are seldom, I believe, scrofulous, and more rarely if ever do ulcers occur upon the uterine neck as the result of simple inflammation, fulfilling the conditions that would entitle them to be admitted into the category of true ulcerations.

Distensions of the uterine cavity, by liquid or gaseous contents, constitute the affections termed respectively *hydrometra*, *hæmatometra*, and *physometra*. These collections result usually from narrowing or atresia of some portion of the vagina or cervix, whereby the natural or morbid secretions of the uterus become pent up in its cavity. They are generally accompanied by hypertrophy, but sometimes by atrophy of the uterine walls.

* Some of these morphological varieties have been described in a preceding page; and such, together with many of the hypertrophies already noticed, have been repeatedly submitted to me during life as examples of ulcers of the uterine neck.

Hydrometra results usually from a combination of chronic uterine catarrh with obliteration, absolute or relative. of the lower uterine orifices. Such obliteration, for example, may be caused by chronic disease of the cervix, by the presence of a submucous fibroid or a cervical polypus obstructing the cervical canal, or by the pressure of an enlarged neighbouring viscus, as the ovary *, or of a chronic abscess. If, with these or similar conditions, uterine catarrh co-exists, the secretion from the mucous membrane collects in, and gradually distends, the cavity; the walls of the uterus becoming at the same time hypertrophied, or sometimes atrophied.† The fluid which accumulates in such cases may be thin and watery, but it is more often puriform, and in some instances, as in Dr. Hooper's example, which resulted from the opening of an abscess into the uterine cavity, it consists of pure pus. To these cases, the term *pyo-metra* would be perhaps more appropriate. Collections of these kinds amount usually to several ounces, or may reach one or two pounds. The uterus enlarges to the size of a fist, and, in rare examples, to the bulk of the gravid uterus at term.‡ Pure hydrometra, *i e.* without hæmatometra, can only occur after the climacteric period, or in combination with amenorrhœa.

When the inner and outer os uteri are both closed, and the cervical and uterine cavities are at the same time distended, the organ resembles an hourglass in form. This constitutes the *uterus bicameratus vetularum* of Mayer.

Hydrometra is to be distinguished from *hydrorrhœa uteri*, in which there is no obstruction, but a continual escape of a thin, watery fluid, often to a large amount. This condition, which may occur both in the unimpregnated and gravid uterus, is apparently dependent upon excessive activity of the follicular structure of the cervix, and may be viewed as a coryza of that part.

Hæmatometra consists in a collection of blood, usually menstrual, in the uterine cavity. It is commonly associated with atresia of the vagina at some point, generally at the orifice, as when the hymen is imperforate, or when the orifice has become closed by inflammation of the vulva in early infancy. Under these circumstances, when the menstrual age arrives, the fluid, for which there is no outlet, collects in, and distends, the cavity of the uterus, whose walls at the same time become hypertrophied, as in pregnancy; or occasionally attenuated, as in the case of hydrometra just stated. The fluid, which is generally dark-coloured, and of the consistence of treacle, may, if not artificially evacuated, escape spontaneously in various ways, viz. into the abdominal cavity, by travelling along the oviducts, or through lacerated or ulcerated open-

* Scanzoni, *loc. cit.* p. 165.
† Hooper, Morbid Anat. of Uterus, pl. III.
‡ Case. Dr. A. T. Thomson, Med. Chir. Trans. vol. xiii.

ings in the uterine walls; or, if previous adhesions are formed, the fluid may escape by the vagina or rectum. Hæmatometra may occur also in certain malformations of the uterus, as already described (p. 680.).

Physometra. Pneumatosis s. tympanites uteri.—This affection, known to Hippocrates* and Aretæus†, consists in a collection of air in the cavity of the uterus, which makes its escape from time to time by the vagina, with or without explosion. The air may be dry, or accompanied by more or less fluid (*physometra humida*). In ordinary cases it is inodorous, but occasionally it possesses a most offensive odour. In these latter cases (*physometra putrida*), the gas appears to be generated by decomposition of some substance within the uterus, as a putrid fœtus, the remains of a placenta left in utero, and the like, while the generation of an inodorous gas, on the other hand, without the presence of any such substances, within the uterus, can only be compared with those sudden developments of air in the stomach and intestines which often take place in hysterical women.

Hydatids.—A case of acephalocysts within the ovary has been given at p. 584., but this is so rare an affection of the uterus that no anatomical collection, I believe, in this city contains an example of it. Rokitansky's often-quoted case‡ appears to be the only certain instance of acephalocysts in the uterine cavity which pathologists in the present day are able to adduce.

In the "Lancet" of 1840, vol. i. p. 691., a case is reported as one of uterine hydatids, the nature of which is not very clear. That they were not acephalocysts (echinococcus vesicles) may be inferred from the description. This case, which is quoted here as an example of the more doubtful instances of hydatids, was probably one of interstitial pregnancy (see p. 621.) combined with the vesicular degeneration of the chorion described in the next paragraph.

Those vesicular masses and groups or strings of watery vesicles, falsely termed hydatids, which are so frequently expelled from the uterus accompanied or preceded by abundant serous discharges, combined with rapid distension of the abdomen and some symptoms of pregnancy, consist invariably of moniliform enlargements of the villi of an imperfectly developed chorion or placenta.

It is almost needless to observe that the presence of a true chorion structure, which these substances invariably exhibit, even in their most degenerated and abnormal forms§, constitutes unquestionable evidence of a prior act of impregnation. Connected with these, when the degeneration is not much advanced, may be sometimes found an embryo perfectly or incompletely developed*, but in higher grades of this abnormal state the embryo invariably perishes or is unformed.

* De Morbis Mulierum.

† De Causis et Signis Morb. Diuturn.

‡ Loc. cit. vol. ii. p. 291.

§ For descriptions and illustrations of these structures see Wedl, Pathological Histology (Syd. Soc.), p. 172.

Narrowing and obliteration of the uterine cavity. Atresia.—The defects which come under this head may be either congenital or acquired. They may consist in a simple narrowing, or stricture of the cavities of the uterus, or of the apertures leading to them, or in a complete obliteration of some or all of these. Probably most of the cases of atresia which do not originate in the malformations already described, have resulted from the organisation of the products of inflammation affecting these parts.

Obliteration of the *external os uteri*, either partial or complete, is the most common of these conditions. In minor degrees, where the form of the parts is not lost in adhesions with adjacent structures, the os is found closed by narrow membranous threads or bands. If the closure is not complete, pregnancy may ensue, but labour is obstructed, and the original seat of the os is then with difficulty traced, or it cannot be found.

The *cervical canal* may be entirely obliterated by the formation of fibrous tissue, in which smooth muscular fibres have been sometimes found.

Obliteration, or narrowing of the *inner uterine orifice*, may occur in the progress of senile atrophy, or as a result of the same processes that cause obliterations lower down. All the foregoing atresiæ may result in the collections of fluids within the uterine cavity recently described.

Lastly, the *cavity of the uterine body* may be so completely closed that no trace of it can be found. Such an example is delineated in Pl. 13. of Boivin's and Dugès' Atlas, which contains also the figure of another uterus, the original seat of whose cavity is indicated only by a narrow triangular band of white tissue nearly as hard as cartilage.

Pathologic conditions which may involve several of the uterine tissues.

Cancer.—The two main disorganising processes by which the structure of the uterus is metamorphosed or disintegrated and ultimately more or less destroyed, are those under which cancer and fibroid are respectively developed in its tissues. Of these, regarded as destructive agents, cancer ranks second in point of frequency, but first in potency.

Cancer occurs in the uterus as in the ovaries, under the three principal varieties of encephaloid, scirrhous, and colloid. But while in the latter organ colloid as a primary disease is certainly more common than either of the other two; in the uterus, on the other hand, both scirrhous and colloid are rare, while encephaloid constitutes the chief form under which cancer is found.

The development of cancer may undoubtedly commence in any portion of the uterus, but the number of instances in which it occurs,

* Granville, Graphic Illustrations of Abortion pl. iv. and v.

first, in the cervix, and especially in the vaginal portion, is so preponderating, that this may be regarded as mainly the seat of origin of uterine cancer.

The comparative rarity of opportunities for examining uterine cancer in the incipient stage, has limited to a certain extent our knowledge of this part of the subject.

The cervix in the incipient stage, smooth, tense and hard, or exhibiting upon its surface here and there knotty projections, is found upon section to have its tissues infiltrated in parts by the cancerous structure, which differs in the character and relative proportions of its elements, according to the form which the cancer assumes. In the medullary variety a white cream-like or lardaceous semi-fluid matter, composed of the usual cancer constituents, is found interspersed among the meshes of a loose reticulum, in the softer portions of which few if any of the normal uterine fibres can be traced. The larger preponderance of the encephaloid matter, compared with the fibrous stroma, occasions that semi-elastic feel which the part early acquires, and at the same time constitutes the main difference between encephaloid and scirrhous cancer.

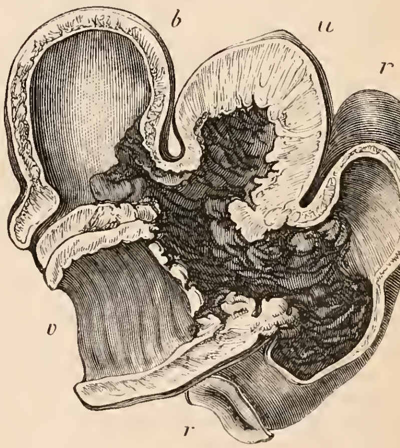
In the scirrhous or fibrous variety the greater hardness of the structures is dependent upon the presence of a large proportion of a coarser fibrous stroma, composed of dense white fibres, the minute interspaces of which are occupied by a greyish or reddish softer and often pulpy substance, which may be obtained by scraping, or may be squeezed from the part. In the harder forms of scirrhous but little fluid is so obtainable; but in some specimens here and there, softer portions are found from which a fluid cream-like matter exudes, differing in no respect from the pulp of encephaloid cancer. These and the softer portions obtained by scraping are composed of cancer cells with molecules, granules, and disintegrated fibrous tissue.

The irregular nodulated projections occasioned by the unequal development of the cancer structure rapidly increase in the encephaloid variety, and the cervix becomes much enlarged. The surface of the more projecting portions becomes florid and vascular, and these portions pass first into ulceration by thinning and absorption of their mucous covering. The creamy or cheese-like contents of these tuberculated portions then escape, and being sometimes of a yellow colour may be mistaken for tuberculous matter.

This stage is followed by the formation of one or more corresponding ulcers upon the outer cervix, which coalescing destroy the remaining portions of the mucous membrane, and spreading up the cervical canal, convert it into an irregular funnel-shaped cavity, bounded below by hard rugged margins. Or fungous vascular growths, friable and easily bleeding, sprout from the part and entirely destroy its natural configuration. A yellow or greenish-brown sanious discharge, of a highly fetid odour, mixed occasionally with florid blood and ultimately with fragments of putrid tissue, dates from the commencement of ulceration, and increases in proportion to the extent of surface denuded. The fragments of putrefied tissue which hang from the ulcerated surfaces, and occasionally pass away in the discharges, consist mainly of connective tissue fibres, which are more slowly disintegrated, stained of a dirty brown colour by infiltration with decomposed blood.

By these disintegrating processes both lips, and finally the cervix itself, are destroyed and removed; the cancer structures being continually deposited in advance of the ulceration, while the fundus and even the body of the uterus may still remain sound. In like manner cancerous deposits take place in the fibrous tissue surrounding the uterine neck, and attaching it to adjacent parts. Thus the uterus becomes fixed in the pelvis, and at the same time a way is paved for the further extension of destructive ulceration, by which first the bladder and then the rectum are penetrated, and the disease further extending down the vagina, the whole is laid open into one ulcerous cloaca (*fig.* 479.). If life is

Fig. 479.



Cancer of the neck of the uterus (*u*), extending to the bladder (*b*), rectum (*r*), and upper part of the vagina (*v*). (*Ad Nat.*)

maintained beyond this point the pelvis becomes lined with cancerous matter, and, the peritoneum inflaming, all the adjacent parts become agglutinated together, until finally the ulceration may extend into and lay open the peritoneal cavity itself.

The penetration of the bladder earlier than the rectum, which almost uniformly obtains, is explained by the different modes of connexion of the cervix with these two parts. Since nothing but fibrous tissue intervenes between the bladder and the anterior cervical wall (*fig.* 426. *b b* and 433 F), the cancer elements are readily deposited, and extended in this direction, while the posterior wall being separated from the rectum by a double fold of peritoneum (*fig.* 426. 433. G), the cancer matter does not so easily penetrate through this, not at least until adhesions have formed.*

But cancer may commence in the fundus or body, instead of in the cervix, although this is rare; or it may extend to the uterus from the ovary. In this way extensive disorganisation of the adjacent parts may occur, the cervix remaining intact.†

Cancer, when thus developed, especially in the encephaloid variety, assumes often the form of distinct masses or tumours, rather than of an infiltration of the tissues.

These tumours may be imbedded in the uterine walls, or form numerous irregular rounded and sometimes pedunculated masses, variously attached to, or projecting from their surface. On the other hand such a distinct mass formed in the substance of the uterine walls, or beneath the mucous membrane, may in the course of growth push the latter before it, and, subsequently acquiring a stem, may fill the uterine cavity or protrude into the vagina, and constitute a malignant polypus.

In most cases of uterine cancer the uterus is the primary, and except in those instances where the disease has spread by direct extension to adjacent parts, it may remain throughout the sole organ attacked. Or uterine cancer may be associated with like formations in the stomach, mamma, ovary, &c., and be developed concurrently with or consecutively to these.

Cancroid. Epithelial cancer. Cauliflower excrescence.— Cancroid of the uterus is limited in its commencement to the vaginal portion of the cervix, and presents the following principal varieties. It may appear under the form of papillary growths, resembling condylomata, which spring from the mucous surface, and form little compact masses that gradually, by the growth and elongation of the papillæ, become soft, pulpy, and brittle, and easily bleed on being touched. After a time a basis of cancroid is developed in the cervical tissues, or the papillary growth appears upon a larger scale, forming a hard, knotty, and brittle mass, which grows with tolerable rapidity, and ultimately more or less fills the vagina or protrudes from the vulva. In form the growth often resembles a cauliflower, to which it was likened by Dr. John Clarke. The surface is of a bright flesh colour, and is covered with small projections or granules. These again are united into larger masses or lobes, set upon short and broad stems, that ultimately coalesce into a common basis formed by one or both lips of the cervix. The whole tumour has a certain firmness and solidity; but the superficial granules are so brittle that slight handling causes some to break away, a free hæmorrhage resulting. Or the cancroid, after being developed in and beneath the mucous membrane of the cervix in the form of little granular masses, gradually breaks through the surface; while in the course of time ulcerations form upon the most prominent portions, and these coalescing, while increased deposits of cancroid take place in the sublying tissues, which in turn are also destroyed, a sore, more or less extensive, is formed that in its further aspect and progress very nearly resembles encephaloid cancer.

Regarding the structure of these cancroid formations, they are, according to Virchow, at the commencement simple papillary growths, and later assume the characters of cancroid. At first they appear in the form of small villous projections from the surface, composed of an outer very thick layer of peripheral epithelial plates, and an inner one of cylinder ephithelium, the interior of the villus consisting of large blood-vessels. These vessels are chiefly colossal thin-walled capillaries, which either form simple loops at the extremities of the villi between the layers of epithelium, or ramify in compound loops over the surface, or lastly, present a retiform arrangement. The great size, tenuity, and superficial position of these vessels explains the profuse discharge of watery fluid, and frequent bleedings, which constitute such striking features in the progress of the cauliflower excrescence, as well as the entire collapse and almost total disappearance of those tumours after death, so that only slight traces of them are found on post-mortem examination.

At the commencement the papillæ are single and close-set, so that the surface, as Clarke describes it, is merely granular. The peculiar cauliflower form is occasioned by the branching of the papillæ, which ultimately form fringes an inch in length. After this superficial process of growth has continued for a certain time, cancroid alveolar spaces begin to be formed at the base, between the fibrous and muscular layers of the organ. At first these appear as simple spaces, with epithelial contents, but later are found alveoli, from whose parietes new papillæ spring, which also become ramified, constituting arborescent proliferous growths.

Corroding ulcer.— Here may be noticed an affection of the uterine cervix, whose exact pathological relations have not been determined with sufficient accuracy. The corroding ulcer, first described by Dr. John Clarke, and compared by Rokitansky to a phagedenic (cancerous) sore of the skin, differs mainly from cancer in the absence of a cancer basis, or of cancerous infiltration of adjacent tissues, while it resembles the destructive march of cancer in its mode of gradually disintegrating, and destroying the os and cervix, and even portions of the body of the uterus, and extending to the bladder, rectum, and adjacent structures. The characters of this ulcer are those of a ragged, irregular-margined sore, with a brownish or greyish base, from which issues a thick purulent or copious watery secretion. The margins and base may be thickened by inflammation, but there are no granulations.

* Dr. West is, I believe, the only author who has hitherto pointed out the true cause of this difference.

† See case, p. 593.

Upon the question of the nature of this form of ulceration Foerster gives a useful hint. After describing a case which fell under his notice, and where he could find no traces of either encephaloid or epithelial cancer in the base of the ulcer, he mentions another which also to the naked eye appeared to have no cancerous basis, and yet on microscopic examination the entire base of the ulcer, to the depth of a line, was found to consist of cancer structure.* May not the thinness of this layer, by limiting the pabulum which feeds the progress of the ulcer, explain the slow advances of the latter observable in some cases of corroding ulcer?

Tubercle rarely effects the uterus, and still more rarely is it a primary disease of that organ.

Tubercle of the uterus exhibits the following peculiarities. The tuberculous deposit is limited in the first instance to the mucous membrane of the body of the organ. Here it occurs either in the form of tuberculous granulations, isolated or collected in groups, or more often as a uniform infiltration, limited at first to the mucous membrane, but ultimately penetrating more or less deeply the sublying uterine parenchyma, and accompanied by hypertrophy of the muscular coat. In the subsequent metamorphosis of the tubercular formation the infiltered membrane softens and melts down, so that the cavity becomes filled by a purulent pulpy fluid. The tubercular infiltration terminates abruptly at the inner uterine orifice†; or if rarely it penetrates the cervical canal or appears upon the vaginal portion, it is then only in the form of isolated tubercular granulations, which latter may probably pass into tubercular ulcers.

Tuberculosis of the uterus is usually associated with a corresponding condition of the mucous membrane lining the Fallopian tubes. These latter are found distended and their canals filled by caseous tuberculous matter.

Solutions of Continuity.

Laceration of the walls of the uterus occurs under various circumstances. It happens rarely in the unimpregnated organ, more frequently during pregnancy, and most commonly during labour.

Rupture of the walls of the unimpregnated uterus can only occur under abnormal conditions of the organ, as from considerable growths of fibroid, or from great distension of the cavity by watery, puriform, or sanguineous fluids, such as occur in hydro- and hæmatometra. See p. 697.

Rupture during pregnancy may happen at almost any period, but chiefly during the latter half, although it may take place even as early as the second month, as from vomiting.‡ Or it may be occasioned by violent spasmodic contraction, or from contusion or sudden concussion. It is most likely to happen in the case of the imperfectly developed uterus, as in the uterus unicornis, of which a description has been already given (p. 679.), or in the case of gestation in the uterine portion of the Fallopian tube (graviditas interstitialis, p. 621.).

Rupture of the uterus may occur upon only very slight exertion, as in the act of stooping*, or even without any obvious cause, as during sleep.† Most of the recorded cases, however, of spontaneous rupture of the uterus have occurred during labour, under violent uterine action, combined with some unusual resistance to the passage of the child, such as is occasioned by a distorted or fractured pelvis, a tumour, an unyielding state of the os and cervix uteri, or by some malposition or unusual bulk of the child. It may also occur from violence in instrumental delivery, or from injudicious efforts to turn the child.

The seat of rupture is most commonly the neighbourhood of the cervix, the laceration extending very often through the os to the vagina, or upwards, so as to involve more or less of the body of the uterus. It occurs oftenest at the sides, less frequently in the anterior or posterior walls, and least of all at the fundus.

The course of the laceration is generally oblique, rarely in the horizontal direction. It may, however, extend round the whole circumference of the cervix, the lower segment of the uterus being forced off in a single piece, before the presenting part of the child.‡

The length of the rupture may be such as to admit of the child escaping into the abdomen, among the intestines, or it may be only very slight. All the coats of the uterus are not necessarily involved. The peritoneum alone may be torn, numerous rents (40—60) occurring in this coat, without extending to the muscular tissue.§

These lacerations occur in most instances where the uterine tissues are perfectly healthy. In some cases the walls of the uterus have been apparently attenuated, the attenuation being attributed to pressure upon the spine or pelvic bones, or there has been more or less evidence of antecedent inflammation near the seat of the accident.

Perforation of the uterine walls occurs in cancer, (*fig.* 479.) followed by the establishment of fistulous communications with the bladder and rectum; or from penetrating abscess at the surface of the uterus; or as a consequence of adhesions formed between the uterus and an ovarian cyst, the contents of

* Handbuch der speciellen pathologischen Anatomie, 1854, p. 318.

† Boivin and Dugès' Atlas, pl. xvi.

‡ Case by Collineau. Journal Gén. de Méd. 1808.

* Mr. Glen's case in the eighth month of gestation, related by Dr. Merriman. Synopsis of Difficult Parturition, 1826, p. 268.

† Mr. Ilott's case, sixth month. Med. Repository, vol. vii.

‡ Mr. Scott's case. Medico-Chirurgical Transactions, 1821.

§ Trans. for the Improvement of Med. and Surg. Knowledge, vol. iii.

the latter being discharged through the uterine cavity.

Pathological conditions of the Uterus after Parturition.

Irregular contraction. — After tedious and exhausting labours, or those in which the uterus has been rapidly emptied, or under other circumstances which tend to the production of a general or partial atony of the organ, its post-partum contractions are often imperfect. The whole uterus may remain relaxed and undiminished in size, or a portion only of the walls may contract while the rest remain inactive. From the latter combination result the hour-glass and other irregular forms of the organ when the cavity of the uterus is partitioned into two chambers, in the upper of which a part or the whole of the placenta may be imprisoned. The seat of constriction being either near the fundus, or the centre of the uterus, or the neighbourhood of the cervix. This condition is often attended by hæmorrhage from the uncontracted portions of the uterine walls.

In explanation of these irregular contractions, it has been usually assumed that the contracted portions consist of the fibres that have retained their vigour, and the relaxed parts of those that have been exhausted. Numerous observations, however, have satisfied me that this is but an imperfect and, in some respects, an erroneous interpretation of this phenomenon. It appears to depend rather upon arrested peristaltic action, which may indeed be, and probably is, the result of exhaustion; not, however, of a particular set of fibres, but of the ganglionic nerves which especially govern this movement of the organ. So that the peristaltic contraction in travelling along the uterus from os to fundus, is stopped in some part of its course. This explanation is consistent with the fact that these constrictions are not confined to any special region, but may occur at any point between the cervix and the fundus, and particularly with the circumstance that in some cases the constricted part may change its seat, the contraction being sometimes felt to travel onwards towards the fundus, while the hand is employed within the uterus in removing the placenta. See p. 673.

Rokitansky describes a remarkable result of partial contraction, with relaxation of the rest of the uterine fibre. When this occurs at the placental region, the part that gave attachment to the placenta being relaxed is forced into the cavity of the uterus by the superior tonicity of the surrounding tissues, and there constitutes a kind of tumour which, on account of its form and the protracted hæmorrhage that usually ensues, may be mistaken for a polypus or a hæmatoid growth.

Retarded and incomplete involution consists in an arrest of those metamorphic processes by which the uterus after parturition is restored to its ordinary condition. All inflammatory puerperal processes are attended by this condition in a greater or less degree. But involution may be arrested without inflammatory action, so that the uterus remains undiminished in bulk, its fibre uncontracted, and its tissues unrenovated for several weeks or months after labour. The soft flabby organ is easily distinguished above the pubes, reaching sometimes as high as the umbilicus; while its cavity, tested by the uterine sound, may measure several inches in depth.

Puerperal inflammations.—The puerperal or post-partum inflammatory affections of the uterus may be noticed according as they involve the peritoneum, the proper tissue together with the blood-vessels and absorbents, or the lining membrane of the organ.

Puerperal endometritis.—Inflammation of the internal surface of the uterus occurs, as a primary affection of that organ, shortly (within a few hours or days) after labour. It takes the form usually of plastic inflammation, whose first seat is either the surface which has been exposed by the separation of the placenta, or certain portions that have suffered injury, such as lacerations and contusions, occurring during forced or spontaneous delivery. From these points, the inflammatory action may spread over the entire inner superficies of the organ, or it may involve more or less deeply the uterine parenchyma, and ultimately extend by contiguity to the peritoneum itself. The form of inflammation, and the nature of the exudative products, exhibit great variations in different instances, variations which are especially observable in respect of individual and epidemic influences, and are directly connected with corresponding conditions of the blood to be hereafter noticed. Endometrial inflammations have been accordingly distinguished by some pathologists, as croupy, dysenteric, catarrhal, and the like.

The exudations of the fibrinous or croupous kind, which are found upon the inner surface of the inflamed uterus, exhibit sometimes great plasticity. These may occur in the form of isolated patches, or of more extensive investments of a dense yellowish or greenish lymph, either firmly agglutinated to, or lying loosely upon, the sublying tissues. In inflammations of a less sthenic type, the exudation is softer and more gelatinous, and is often intermixed with serous and purulent fluids. Or the fibrinous matter may be wholly wanting; the inflammatory products consisting then entirely of purulent discoloured and sanious exudations, which, in cases that have been distinguished as putrescence of the uterus, assume usually a greenish or dirty-brown coffee-coloured aspect.

The condition of the tissues, which are brought into view by removing or wiping away the above-mentioned products, exhibits corresponding variations. Beneath the coating of firm lymph, characteristic of uterine croup, the uterine tissue is merely softer and more spongy, and redder than usual; but in those forms of inflammatory action which rapidly pass into the puriform stage, the subjacent tissues become infiltrated and softened, so that they may be easily scraped away in the form of a discoloured flocculent pulp. This condition, in its highest degree, where the tissues appear macerated and deeply penetrated by the dirty-coloured fluids already described, at the surface, constitutes uterine putrescence.

In addition to these products and results of inflammation, there may be found attached to the uterine surface fragments of an imperfectly detached placenta, or blood clots and shreds of the deciduous lining, lying free within its cavity. These, by their decomposition within the uterus, whose cavity, from the moment of parturition, has ceased to be completely closed against atmospheric contact, play an important part in the production of those septic and other infections of the blood which appear to form an essential part of all or nearly all puerperal inflammatory processes.

Puerperal metrophlebitis.—Inflammation of the veins of the uterus occurs most frequently in combination with, and is, to a certain extent, secondary to, the conditions last described; but it may occur also as a primary affection, and continue for a time the chief or only morbid state of the organ. The inflammation is seldom confined throughout to the veins of the uterus. It appears to commence in some of the orifices of the venous sinuses, which, after labour, terminate open mouthed upon the inner surface of the uterus, over the placental place, and thence spreading through those sinuses which occupy the uterine walls, it may extend to the spermatic and hypogastric veins and their tributaries, either upon one or both sides, and ultimately involve more distant vessels.

The condition of the veins in uterine phlebitis varies according to the intensity and duration of the inflammation. The inner coat may be pale or stained with the colouring matter of the blood. It may have lost its polish, or have become adherent to the contents of the vessel, where these are of a solid nature. The coats of the vessels affected may be thickened and opake, and the surrounding tissues infiltered by various colouring fluids, or softened and in a state of putrescence.

Regarding the contents of the vessels, these consist sometimes of firm plugs of fibrine coagulated from the blood, but more often of these in a softened grumous state, intermixed with portions of a yellow grey or whitish colour. The interior of such coagula may consist of a fluid not easily distinguishable from pus, but resulting from metamorphic changes in the fibrine, subsequent to its coagulation within the vessels. Or the veins may be distended by a brownish sanies, or a yellow or greenish yellow viscid pus, so that upon section of the uterine walls numerous collections of the latter, resembling separate abscesses, are displayed.

In the more severe cases of metrophlebitis the proper tissue of the uterus is deeply involved, being discoloured and in a state of disorganisation and putrescence throughout its entire thickness; or exhibiting at different points smaller or larger abscesses, the contents of which may have been discharged into the general cavity, or form ramified sinuses or fistulæ in the uterine substance. Such abscesses most probably arise from the suppurative inflammation extending beyond the coats of the veins, and involving the surrounding parenchyma.

Uterine phlebitis is often associated with inflammation of the uterine lymphatics (*Lymphangioitis*). These vessels, like the veins, become distended and varicose, and filled with a yellow or greenish puriform fluid, so that their course, together with that of the Fallopian tubes and ovaries, which are generally conjointly affected, may be easily traced into the corresponding hypogastric and lumbar lymphatic plexuses and glands.

Puerperal metro-peritonitis, or inflammation of the peritoneal coat of the uterus, is associated with either or both of the foregoing affections, or it occurs as the primary local disease, and sometimes constitutes throughout the sole apparent morbid condition of the uterus. The inflammation may be limited to the peritoneal covering of the uterus and its appendages, or it may involve that of the entire pelvic and abdominal regions. The membrane itself, which often exhibits little vascular congestion, may have retained its polish, or may be covered by exudative products of very various characters. These may be only small in amount, and partially distributed, or abundant and copious. They consist of firm fibrinous concretions, or softer and more pulpy yellow or greenish exudations, consisting of coagulable lymph loosened by serous or purulent infiltration, or thick purulent fluid, or semi-fluid matter, or lastly serous or sanious fluids, the latter being often discoloured and rendered turbid by intermixture with the before-mentioned products, especially with fibrinous flocculi and puriform and sanguineous effusions.

These several pathological conditions of the uterus, which appear to be incompatible with the progress of those normal changes in the condition of the organ that constitute the process of involution (see p. 658.), are accompanied almost invariably by a marked interference with those processes, so that the act of retrogression is either altogether arrested, or is in a high degree retarded.

The foregoing puerperal affections of the uterus exhibit numerous points of great pathological interest. These, even in their milder forms, cannot be generally regarded as purely topical affections, for they commonly, in their progress, become associated with like conditions of other and often distant organs, whose connection with the original, or at least principal, seat of disease, can only be explained upon the hypothesis of a general dyscrasis of the blood. It is probable that in some cases, of those, for example, whose commencement is apparently dependent upon miasmatic influences, inoculation with cadaveric matter and the like, a primary infection of the blood precedes the development of the topical condition, which may be viewed as the local expression of the former. In a large number of instances, however, the affection of distant parts may be considered as the result of a secondary blood infection, *i.e.* of a poisoning of the blood by the introduction of some products from the original nidus of disease, and particularly of venous pus and sanies in metrophlebitis.*

The occurrences which immediately ensue upon the act of parturition, offer a ready explanation of the mode in which these and other extraneous matters may gain access to the general circulating fluid. For by the separation and removal of the placenta, together with a large portion of the decidua, the contents of the uterine cavity, consisting of various puerperal products now exposed to the direct influence of the atmosphere, are brought into immediate relation with the patent orifice of the uterine veins terminating upon the placental space. Through these a copious reception of the exudated products of inflammation or of septic matters resulting from decomposition within the uterus, or of infecting matter derived from sources still more external, may readily take place, and so produce either the primary or secondary dyscrases of the blood just noticed.

It is also to be observed that independent of external sources of a blood dyscrasis, the latter may be occasioned by an accumulation of effete material, resulting from the arrest of those eliminative processes which constitute so large and important a part of the act of involution, and are always more or less impeded during puerperal inflammation; or commonly by a reflux of pus and sanies formed in the larger venous channels in the case of metrophlebitis already mentioned; while some of the worst forms of sepsis of the blood are those which result from deep prostration of the nervous system, occasioned by exhausting forms of parturition.

The more important associated morbid processes occurring in connection with puerperal inflammation of the uterus, which it may be necessary here to notice, consist in exudations into the larger serous sacs and synovial bursæ, upon the mucous membranes, and in the parenchyma of various parts and organs; and of deposits within the larger vessels, chiefly the veins leading from the uterus, or in the capillaries of organs often far removed from the original seat of inflammation.

The effusions upon the peritoneum and pleura, and less frequently upon the pericardium, consist of fibrinous and croupous exudations, combined often with copious effusions of serous, purulent, or sero-purulent fluids, the latter being, perhaps, often the result of a breaking down or liquefaction of the croupous fibrine, and its conversion into a pus-like fluid. Similar collections are found in the synovial membranes of the larger joints, especially of the knee, shoulder, and hip. While upon the mucous surfaces, particularly of the intestines, which are later affected than the serous structures, a less sthenic form of exudation is usually found, the effusion consisting here of serous, gelatinous, or purulent exudations (the former contributing largely to the production of puerperal diarrhœa), and of infiltrations into the mucous and submucous areolar tissues.

These various exudative processes, whose preference for particular tissues is probably in part determined by textural peculiarities, must be considered as efforts to eliminate the dyscrasial materials from the general blood mass, and they will continue until the exhaustion of the crasis is complete.

The qualitative variations observable in the products bear exact relation to the nature of the previous infection, and of the dyscrasis arising out of it. The character and mode also of the first effusions may materially affect those which occur at a later period; for when the plastic products have been very abundantly and rapidly formed, and the defibrination of the blood consequently very considerable, the extensive discharge of the fibrinous element leaves the blood so attenuated, that the serous portion may then speedily transude through the walls of the capillary vessels, and in this way are produced those enormous collections of serous or sero-purulent fluids which sometimes rapidly form in the advanced stages of puerperal inflammations, occasionally with but slight evidences during life of their occurrence.

Of equal or greater interest are those associated pathological phenomena which are connected with secondary phlebitis, having its seat either in the larger veins, or in the capillary system of vessels. The veins nearest to the uterus are commonly first involved; and from this point the inflammatory action may spread either by direct or interrupted continuity to more distant vessels, following, however, the reverse order of the circulation; or it affects vessels remote from the original seat of inflammation, as in the capillary congestions, and inflammations of distant parts producing the lobular infarctions, and in more advanced inflammatory stages, the so-called metastatic abscesses and sloughs of various organs and tissues. The obstruction to the circulation arising in these cases from coagulation of fibrine within the vessels, and viewed by some pathologists as the cause, and by others as an effect only of inflammation, may be perhaps regarded as a provision for limiting the spread of the infecting fluids, and preventing, to a certain extent, their introduction into the general circulation.

In the larger vessels, especially in the veins nearest the point of primary infection, the fibrine is found under various conditions of coagulation, forming long cylindrical plugs, as in crural phlebitis, or shorter clots, whose red coloration depends upon the degree in which the blood corpuscles may have been incorporated in its several laminæ, or their paler yellow colour, upon the absence of the same, and the consequent greater purity of

* Rokitansky, *op. cit.* vol. ii.

the (perhaps effused) fibrine. The centre of these coagula may be found softened, and containing the creamy pus-like fluid which results from the molecular disintegration and liquefaction so commonly observed in fibrinous clots. Frequently the clots are of a less consistent texture, being of a dark brown or chocolate colour, or reduced to the consistence of a soft pulp. The coats of the veins may be thickened and adherent to the contained coagula, or covered by fibrinous laminæ or merely blood-stained, or presenting no deviation from the natural state.

LIGAMENTS OF THE UTERUS.

These terms are applied to several duplicatures of peritoneum, containing variable quantities of fibrous and muscular tissue, which serve to connect together the uterus and its appendages and to limit the motions of these parts within the pelvis. They are distinguished as the *broad*, the *round*, the *utero-sacral*, and the *utero-vesical* ligaments.

The broad ligament.— The fold of peritoneum in which the uterus is contained, after investing the fundus and anterior and posterior walls of the organ, passes off laterally in the form of a double lamina that extends from each uterine border horizontally outwards as far as the sides and base of the pelvis, to which it is attached. Thus a vertical septum is formed, which divides the cavity of the pelvis transversely into two chambers; the anterior and shallower one containing the bladder, the posterior and deeper holding the rectum and a portion of the small intestines. The uterus occupies the middle of the septum, while the lateral extensions of it form the *broad ligament* of either side. *Figs.* 368. and 404. *f.*,

Attached to the upper border of the broad ligament are three folds, termed lesser wings. The central and superior of these, which is the largest, contains in its free falciform edge the Fallopian tube, and at its base a portion of the parovarium. It has been already described as the mesentery of the tube. The smaller posterior fold invests the ovary together with its proper ligament; while the third or anterior fold is inclined obliquely towards the body of the uterus, and constitutes the covering of the round ligament. Between the laminæ which form the principal or lower portion of the broad ligament, as well as within the alæ, are found the blood-vessels, lymphatics, and nerves which supply the uterus and its appendages, together with a variable amount of fibrous and unstriated muscular tissue that serves to connect the alminæ together.

This structure should be regarded as a mesentery rather than a ligament of the uterus. It serves to invest the uterus and its appendages with a common peritoneal covering, and to protect these parts and attach them to the pelvis, as the mesentery attaches the intestines to the spine; while the interspace of the folds suffices for the conveyance of vessels and nerves. The resemblance to a mesentery is more obvious in the bicorned and intestiniform uterus of the mammalia generally, as well as of many other vertebrata in which it forms the *mesometrium.*

The utero-sacral ligaments.— From the posterior wall of the uterine neck two falciform folds of peritoneum proceed towards the rectum. These are most easily seen when the parts are stretched. Between them lies the depression of variable depth known as the retro-uterine pouch, or space of Douglas. When the peritoneum is removed, these folds are seen to be occasioned by two corresponding bands of fibrous tissue, extending from the substance of the cervix backwards towards the sacrum, to which they are attached. Their strength varies considerably in different subjects; so that when not much developed they may be overlooked. The importance of these ligaments, or rather fibrous bands, has perhaps not been generally sufficiently appreciated. From their position and connections it cannot admit of doubt that they are intended to restrain the motions of the uterus, — to prevent it from being forced upwards in the act of conjunction, and especially to limit the descent of the organ in erect postures of the body.

The utero-vesical ligaments. — Opposite to the point of junction of the body and neck of the uterus, where the peritoneum is reflected forwards on to the bladder, are commonly observed two slighter lateral folds, containing bundles of fibrous tissue. These constitute the anterior or utero-vesical ligaments.

The round or sub-pubic ligament: ligamentum rotundum, ligamentum uteri teres. — This ligament consists of a flattened chord or band of muscular and fibrous tissue, which, traced from below upwards, proceeds from the internal inguinal ring in a curved direction towards the superior angle of the uterus on either side, where it is inserted in front of and a little below the commencement of the Fallopian tube. (*Figs.* 404. and 418.) The ligament of the right side is commonly shorter than that of the left: hence it happens that in pregnancy the uterus more often inclines to that side. According to Mr. Rainey*, the round ligament arises by three fasciculi of tendinous fibres: the inner one from the tendons of the internal oblique and transversalis muscles near the symphysis pubis; the middle one, from the superior column of the external abdominal ring, near its upper part; and the external fasciculus, from the inferior column of the ring, just above Gimbernat's ligament. From these attachments the fibres pass backwards and outwards, soon becoming fleshy: they then unite into a rounded chord, which crosses in front of the epigastric artery, and behind the lower border of the internal oblique and transversalis muscles, from which it is separated by a thin layer of fascia continuous with the fascia transversalis: it then gets between the layers of peritoneum forming the broad ligament, along which it passes backwards, downwards, and inwards to the point of insertion already described.

* On the Structure and Use of the Ligamentum Rotundum Uteri, Phil. Trans. p. 515. pt. ii. 1850.

The round ligament is composed of smooth muscular fibre, derived from the uterus, and arranged in bundles, surrounded by connective tissue, of striated muscle, continuous with that of the abdominal parietes, and of blood-vessels, lymphatics and nerves.

The peritoneal covering of the round ligament is occasionally prolonged in young subjects at its lower part through a portion of the inguinal canal, where it forms the *canal of Nuck*. This is usually obliterated in adults, where the arrangement of the *tendinous part* of the round ligament just described serves to close the internal ring, and to prevent, in a great measure, the occurrence of inguinal hernia in the female. The persistence of this canal probably leads to the abnormal descent of the ovary into the labium, constituting hernia of the ovary (see p. 574.);—an occurrence exactly comparable with the normal descent of the testis into the scrotum of the male.

VAGINA.

Normal Anatomy.

Syn. Vulvo-uterine canal. — The vagina constitutes a flattened cylindroid, extending from the vulvar orifice to the neck of the uterus. It lies entirely within the pelvis, between the bladder and rectum, running very nearly in the direction of the axis of the pelvic outlet, but having a slight curvature forwards. The orifice of the vagina is bounded anteriorly by the vestibule, laterally by the nymphæ, and posteriorly by the hymen. The upper or blind extremity, termed the fornix, receives the vaginal portion of the uterine neck, which is not placed exactly at the termination of the canal, but appears as if it were let into its upper wall (*fig.* 433.).

Dimensions.—The vagina is capable of considerable extension. It varies in dimensions in different subjects. In the ordinary virgin state, the anterior wall, which is the shorter, measures, from the median tubercle of the vagina to the anterior lip of the uterus, less than two and a half inches; and the posterior wall, from the centre of the vulvar orifice to the end of the fornix, three inches. The transverse diameter, in the natural state of the canal, which is flattened from before backwards, so that the anterior and posterior walls are in contact, measures ordinarily one inch and a quarter. But when the canal is distended, and after the birth of many children, these dimensions may be much exceeded.

External surface.— The following are the relations of the external surface of the vagina. *Anteriorly*, it is connected to the urethra and base of the bladder by areolar tissue. *Laterally*, it is in relation with the root of the broad ligament and the pelvic fascia. *Posteriorly*, in the first part of its course, it is covered by the peritoneum, forming the anterior wall of the retro-uterine pouch, or space of Douglas; secondly, where the peritoneum ceases, and for about half its course, it is united to the rectum; and lastly, it is separated from the latter by the thickness of the perineum.

Composition. — The walls of the vagina are of variable thickness in different parts, the average being 1‴. They are composed of three coats. The outermost of these is formed of fibrous tissue, intermixed with an abundance of elastic fibre. Beneath this is a second or muscular coat, containing unstriped muscular fibre and fibre-cells, which, during pregnancy, undergo a development similar to that of the uterine fibre. The third, or innermost, is the mucous coat, composed of a dense connective tissue, with much admixture of elastic fibre, to which is due a great part of that elasticity and distensibility with which the vagina is endowed. Imbedded in the substance of the mucous membrane, which is covered by squamous epithelium, are numerous muciparous follicles.

Internal surface.—Upon the inner surface of the canal the mucous membrane is thrown into folds, which, in the virgin, form numerous closely-set transverse rugæ, that are arranged with a certain approach to regularity, and sometimes exhibit a central connecting line or raphé, forming the *columnæ rugarum*, upon the anterior and posterior walls. At the sides of the vagina these folds are less prominent, and take an oblique or longitudinal direction. In some subjects the rugæ are covered by, or are chiefly composed of, short, crowded verrucose papillæ, intermixed with others more filiform. They become larger towards the vaginal orifice, where they sometimes take the form of little leaflets, resembling the smaller fimbriæ of the Fallopian tube, especially about the meatus urinarius. After numerous acts of parturition, as well as from frequent intercourse, the folds become obliterated, and the inner surface of the vagina is rendered nearly or entirely smooth.

Arteries.—A special artery usually exists for the vagina, which may arise either from the hypogastric, internal pudic, middle hæmorrhoidal, or even from the obturator. From one of these origins the artery descends along each side of the vagina, giving off in its course numerous branches, which inosculate in the recto-vaginal septum with those of the opposite side. Near its extremity, the artery sends off a considerable branch to the bulb of the vagina, and after supplying the external organs, it terminates by inosculating with the artery of the opposite side, between the vagina and rectum. One or two separate branches are generally found to arise from the uterine artery. These descend between the bladder and the vagina, supplying branches to both those parts. An abundant and intricate network is formed in the vaginal walls by the ramifications of the smaller vessels derived from these sources, which interpenetrate the several coats down to the mucous membrane.

Veins.— The veins which collect the blood from the labia, constrictor muscles, and mucous membrane of the vagina, and from the erectile tissue forming the vaginal bulb, unite to form a considerable plexus, especially around the vulvar orifice termed the vaginal plexus. From this plexus branches pass to the vesical, and hæmorrhoidal, and uterine plexuses; the blood being finally collected by large veins which empty themselves into the internal iliacs. *Figs.* 482. and 483.

The *Lympatics* are those which are common to the bladder, cervix uteri, and lower part of the rectum. They terminate in the pelvic glands.

The *Nerves* are derived from the pelvic plexus, which contains a large proportion of tubular fibres, derived from the fourth and fifth sacral nerves.

Uses of the vagina. — The vagina, during copulation, serves for the reception of the male intromittent organ, and for the lodgement of the seminal fluid in such a position as to facilitate the introduction of that fluid into the uterus.* During menstruation the vagina gives passage to the catamenia. In labour it transmits the fœtus and secundines, and subsequently the lochia.

Abnormal Anatomy of the Vagina.

Anomalies. — Congenital absence of the vagina is not very rare. The entire vagina may be wanting; so that on separating the labia no trace appears of a canal leading to the uterus; or the canal may be so narrow as only to admit a probe or quill; it may be very short, terminating in a *cul de sac*, or it may open into the urethra or rectum. The latter malformation has not always prevented pregnancy, even when combined with an entire absence of the external organs.

A vertical septum occasionally divides the vagina through a greater or less portion of its course. This, when complete, produces the double vagina with double hymen (*fig.* 461.). The septum may cease at a variable distance from the vaginal orifice, the fornix and upper part remaining single; or, contrarily, the fornix may show signs of division, while the lower part of the tube remains single. The septum is almost invariably in the median line, but the more frequent use of one or other channel in parturition or sexual conjunction may give to them an appearance of unequal development.

Transverse membranous septa sometimes pass across and obstruct the vagina more or less completely. These, though they do not necessarily prevent impregnation, for they are seldom absolutely imperforate, may so far impede labour as to require division. They occur at various points within the canal; at a short distance from the orifice, or as high up as the level of the utero-sacral ligaments. They consist, for the most part, of natural folds unusually developed, or they result from accident, as inflammation or injury consequent on difficult labours. Some of those constrictions which occur near the orifice are doubtless the consequence of inflammation of the vulva and vagina in infancy.† Atresia of the vagina may thus be acquired, or it may be congenital. When the obstruction is complete, retention of the menstrual fluid results.

Displacements. — The vagina may be altogether displaced from the pelvis, or it may simply have its normal direction altered within that cavity. Prolapsus of the vagina occurs sometimes alone, but it is more often combined with procidentia or inversion of the uterus (*fig.* 469.). In any of these cases, if the prolapse is permanent, the vaginal surface loses altogether the character and appearance of a mucous membrane, acquiring a thick cuticular covering, and assuming the condition of ordinary integument. In retroversion of the uterus, the vagina is drawn upwards and forwards, its extremity lying behind the pubic symphysis. (*Fig.* 468.) In hernia of the uterus, the vagina is diverted from the median line towards one or other side of the pelvis, and may be partly included in the hernial sac.

Solutions of continuity. — Laceration of the vaginal walls may occur during obstructed labour, and is then frequently associated with rupture of the uterine cervix. Fistulous openings into the bladder, and sometimes into the rectum, are occasioned by sloughs consequent on protracted labour. Fistulous cloacæ are also commonly formed in advanced stages of cancer (*fig.* 479.).

Inflammation of the vagina. — *Vaginitis.* — This occurs both in the acute and chronic form. It may present the character of benignant catarrh, or of a specific blenorrhœa (*gonorrhœa*). In the more acute form the mucous membrane is highly vascular, and is sometimes excoriated, from excessive shedding of epithelium. The discharge presents variable characters, from the viscid yellow puriform mucus, to the creamy, milk-like, or thin, nearly watery, fluid (*leucorrhœa*).

Croupous exudations occasionally form upon the vaginal mucous membrane, chiefly in connexion with typhoid exanthematous or puerperal processes.

Epithelial desquamation. — Occasionally the entire epithelial coat of the vagina is thrown off, forming a membranous cast of that canal. Several of these casts may be found, one contained within another. Their discharge may be accompanied by symptoms resembling those of dysmenorrhœa; but more particularly by an intolerable itching or sensation of crawling in the vagina. They are composed entirely of dense vaginal tesselated epithelium.*

Serous and sanguineous infiltration into the mucous and fibrous coats of the vagina takes place occasionally during protracted labour, producing considerable tumefaction, and consequent narrowing of the canal. In this state

* See Insemination, p. 671.

† These cases are sometimes recorded as examples of imperforate hymen.

* I have given a description, with several illustrative figures, of these epithelial casts of the vagina, some of which include also the epithelium of the vaginal portion of the cervix uteri, in Beale's Archives of Medicine, for April, 1858. I suspect that the nature of these has been overlooked, and that they have been confounded with the true dysmenorrhœal membranes which consist of the lining membrane of the uterus. See *fig.* 443.

the vaginal walls are easily lacerable, or if subjected to continued pressure pass readily into gangrene.

Abscess forms occasionally in the vaginal walls, but many of the abscesses which burst into that canal have their origin in pelvic cellulitis, or in inflammation of other structures external to the vagina.

Ulceration. — The minute aphthous ulcers which are dotted over the surface of the vagina originate in follicular inflammation. The more extensive and irregular ulcers, except those which form upon the more exposed parts when the vagina is inverted, as in procidentia uteri, are usually either syphilitic or cancerous.

Gangrene of the vagina occurs in conjunction with gangrene of the vulva in septic puerperal processes; or it results from pressure in protracted labour. Spontaneous gangrene occurs also occasionally in infants and young children.

Cysts and tumours. — The former, if of small size, may result from obstructed mucous follicles; but more often the larger cysts arise in situations external to the vagina, and protrude into its canal. In the same way, fibrous or osseous tumours growing from the periosteum or ligaments of the pelvis, ovarian, or even uterine tumours may, by pushing before them the walls of the vagina, protrude into the canal. Vaginal cystocele and rectocele occur in a similar manner. The tumours which lie free within the vagina are chiefly uterine polypi, or cancerous tumours of the cervix or of the vagina itself. The uterus, when partly inverted, also forms a tumour occupying the vagina.

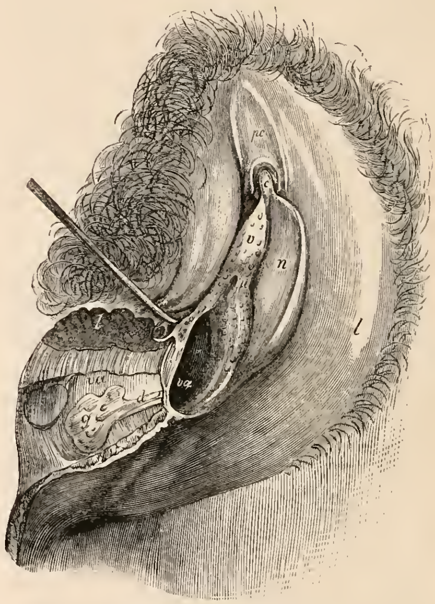
Cancer may originate in the vagina, although it more often constitutes an extension of the same disease from the uterus. In either case it appears most commonly as medullary cancer, taking the form of tuberculated masses or ridges, which narrow or obstruct the passage, and quickly pass through the stages that characterise the ordinary progress of uterine cancer. The surrounding parts become infiltrated with cancer matter, and the vagina is fixed in the pelvis, ulceration of the walls and fistulæ resulting. Occasionally, at the commencement, this disease appears in the form of soft, rapidly-growing papillary structures, springing from the upper and posterior wall of the vagina (*villous cancer*).

EXTERNAL ORGANS OF GENERATION.

Syn. *Vulva. Pudendum.*— These parts perform subordinate offices in the act of reproduction. They are in no way concerned in gestation, and only slightly in menstruation and parturition. They are associated with the vagina in the act of copulation, which has for its object insemination, or the conveyance of the seminal fluid to the internal or formative organs. The parts which serve to establish this relation between the sexes, with the exception of the vagina, are placed external to the body, and are attached to the front of the pelvis. They are included under the general term *vulva* or *pudendum*, which extends from the mons veneris to the perineum. The vulva consists of the following parts, viz. labia, clitoris, nymphæ, vestibule, vaginal orifice, and hymen.

The Mons Veneris forms a slightly rounded or flattened eminence, of triangular outline, covering the symphysis and horizontal rami of the pubes. In fat subjects it is separated from the abdomen by a transverse furrow. It is composed of adipose and fibrous tissue, covered by integument. The latter contains many sebaceous and hair follicles. The hair is not developed until the age of puberty.

Fig. 480.



External organs of generation, and commencement of vagina. (*After Huguier.*)

l, labium of left side (that of the right side is divided and partly removed to expose the vagina and vulvo-vaginal gland); *n*, nympha; *c*, glans clitoridis; *p c*, preputium clitoridis; *v*, vestibule; *u*, orifice of urethra; *v a*, vagina; *g*, vulvo-vaginal gland, or gland of Bartholin and Duvernay; *d*, duct of the same.

The Labia, termed also *labia majora*, to distinguish them from the lesser labia or nymphæ, are two symmetrical tegumental folds (*fig.* 480. *ll*), placed one on either side of the *rima* or fissure which leads to the vagina. The labia vary considerably in size and form in different subjects. In stout adults they are full and fleshy, closing the vulvar orifice, and concealing the rest of the generative organs, which they serve to protect. In the aged the labia become shrivelled and the nymphæ protrude between them, as they also commonly do in infants and young subjects. The outer surface of each labium is composed of common integument, which at the age of puberty becomes covered with hair. Along the line of apposition of the two labia, where the rima is formed, the hair and integument cease, and the mucous membrane common to the rest of the generative canal commences. From this point inwards the surface of the labium is smooth, of a reddish or pink colour, and is here furnished with numerous muciparous and sebaceous follicles, which bedew the parts with an odorous secretion, and preserve their constant moisture. The labia are united above by a slight frenulum, termed the *anterior commissure*, while below they are connected, at the anterior margin of the perineum, by a broader *posterior commissure*. When the parts are here drawn asunder, a second fold appears within the former, just below the entrance of the vagina. The transverse boat-shaped furrow between these constitutes the *fossa navicularis*. Beneath the cutaneous and mucous covering of the labia is found a layer of *dartoid* tissue, the rest of their substance being formed of loose *fibrous and adipose* tissue.

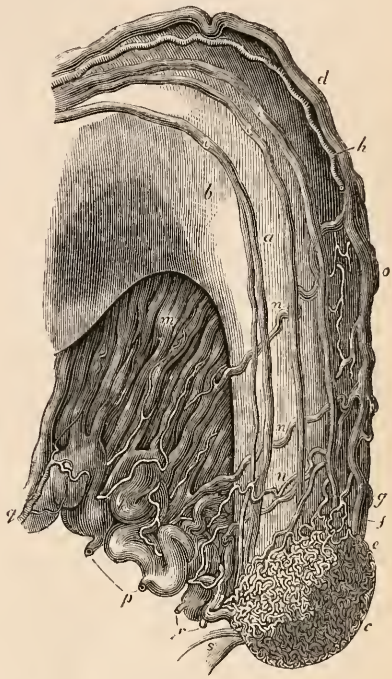
The labia represent the scrotum, which in the early fœtus is divided into two halves. A raphé indicates in the male the line of their subsequent confluence. In the female the two halves remain permanently separate. The normal descent of the testis into the scrotum in the male, about the seventh month of intra-uterine life, is represented by the abnormal descent of the ovary into the labia of the female which constitutes ovarian inguinal hernia. (See p. 574.)

When the labia are drawn asunder, the clitoris, the vestibule, nymphæ, and vaginal orifice are brought into view.

The Clitoris (*figs.* 481. and 482.), in general form and composition, resembles, on a diminutive scale, the penis, but it is deficient in some of the parts which compose the latter organ. The clitoris lies in the upper part of the vulvar fissure, concealed between the labia, and encased in a fold of mucous membrane, the lower border of which forms a hood or prepuce (*preputium clitoridis*) (*fig.* 480. *p c*), that terminates just above the superior commissure of the nymphæ, and allows the extremity only of the organ to appear. When this covering is removed, the clitoris is seen to consist of the following parts: viz. a small imperforate *glans* (*fig.* 481. *c*), composed of spongy erectile tissue, and covered by a highly sensitive mucous membrane, which is abundantly supplied with nerves; this terminates the free extremity of the organ: a *body* (*fig.* 481. *b*), consisting of two *corpora cavernosa*, united along the median line, and invested by a fibrous tunic. The body extends upwards and backwards to a point a little above the centre of the pubic arch. Here it makes a sudden downward curve, and, after dividing into two *crura*, is attached by these beneath the iscio-pubic rami of either side. Opposite the point of curvature, a flattened *suspensory ligament* attaches the body of the clitoris to the pubic symphysis. Two ischio-cavernous muscles (*erectores clitorides*), composed of striped muscular fibre, are inserted into the crura. They have the same relations, and, according to Kobelt, are fully as long as in the male (*fig.* 483. *n*).

Blood-vessels.— Two *dorsal arteries* (*fig.* 481. *h*), running along the upper surface of the clitoris, supply the glans, from which the blood is again collected by superficial veins, emerging from the root of the glans at *e*, and by others having a deeper origin at *f*. These transmit the blood to the *vena dorsalis*, *d*. From the cavernous bodies the blood is also collected by a series of vascular canals, of which an account will be presently given.

Fig. 481.



The clitoris (enlarged 4 diameters.) (After Kobelt.)

a, body; *b*, angle or curvature; *c*, glans; *d*, vena dorsalis; *e*, superficial veins emerging from the root of the glans, and *f g*, veins of deeper origin. These transmit the blood to the vena dorsalis; *h*, dorsal artery; *i i i*, dorsal nerves; *k*, the venous plexus, termed pars intermedia (shown also at *d*, *fig.* 482., and *e*, *fig.* 483.); *l*, communicating venous branch between the glans clitoridis and pars intermedia; *m*, ascending venous canals proceeding from the pars intermedia (*k*) to the under surface of the body of the clitoris; *n n* and *o*, lateral branches of communication between the vessels last named and the vena dorsalis; *p*, veins from the labia, and *r*, from the nymphæ and frenulum clitoridis, which enter the pars intermedia; *q*, arterial branches corresponding with the pars intermedia and communicating veins; *s*, frenulum clitoridis.

Nerves.— The clitoris is richly endowed with *nerves*, *i i*, which are *relatively* three or four times larger than those of the penis. They pass along the sides of the clitoris, each dividing usually into three branches, the ultimate ramifications of which lose themselves partly in intricate plexuses within the glans, and partly in terminal loops upon its mucous covering.

Development. — In the fœtus of three to four months, the clitoris is scarcely distinguishable from the penis. But about the latter period the proportionate retrocession of the one organ, and the increased development of the other begin to be apparent. In the male, the groove along the under surface of the penis is closed in, and at the same time the raphe of the scrotum is formed; while in the female, the parts corresponding with the bulb and corpus spongiosum urethræ remain open, and constitute a portion of the rima. These lie in two halves on either side of the entrance of the vagina, while the urethra is developed independently of them.

Nymphæ.—*Labia minora v. interna.*—These consist of two thin and slightly fleshy folds of mucous membrane (*fig.* 480. *n*), somewhat resembling a cock's comb, which lie on either side of the entrance to the vagina, extending from the clitoris downwards, as far as the middle or lower border of that orifice. The nymphæ commence above by two roots. The inner one, thin and membranous, is inserted beneath the glans clitoridis, and forms with its fellow a kind of *frenum.* The outer one, more fleshy, passes round the glans, and by its junction with the corresponding portion of the opposite side constitutes the *preputium clitoridis* (*fig.* 480. *p c*) already described. From these two roots or origins each nympha extends downwards and outwards, forming a thin prominence, of variable extent in different subjects, until it becomes merged in the labium of the corresponding side, near its posterior extremity.

The nymphæ are composed almost entirely of mucous membrane, which on their outer side is continuous with that of the labia, and upon their inner surface with the lining membrane of the vagina.

Various uses have been assigned to the nymphæ. One of these is that they serve to direct the stream of urine issuing from the urethral orifice, as suggested in the classic allusion to the sea nymphs pouring water from a vase which is implied in their name. Another supposition is that the nymphæ aid the enlargement of the vaginal orifice, by becoming unfolded at the time of labour, although no such unfolding can be absolutely observed. It is more probable that their office is that of extending the secreting and sensitive surfaces at the entrance of the vagina.

The nymphæ correspond with that part in the male which forms the tegumental covering of the urethra, but which remains ununited in the female along the median line.

The Vestibule. — This term has been employed in two senses. In its widest sense it includes all the parts which immediately surround the vaginal orifice. In a more restricted meaning, it is limited to that triangular patch of mucous membrane (*fig.* 480. *v*) which fills up the summit of the pubic arch. In the latter sense the apex of this triangle is formed by the clitoris, the sides by the upper halves of the nymphæ, and the base by the roof of the vaginal orifice. In the centre of the base is situated the *meatus urinarius*, which forms here a slight prominence (*fig.* 480. *u*), at a distance of one inch behind the clitoris. Immediately below this point the anterior column of the vagina terminates in a prominent bulb or tubercle, marked usually by numerous transverse folds.

Orifice of the Vagina, and Hymen.—Immediately below the vestibule, and between the nymphæ, is the orifice of the vagina (*fig.* 480. *v a*), which, in its undistended state, has the form of a vertical fissure, especially in women who have borne children, but in virgins it is more constricted and circular, and is further narrowed by a fold of the vaginal mucous membrane, the *hymen*, which either encircles or semi-encircles the orifice. As some important questions in obstetric and forensic medicine relate to this membrane it will receive here a more particular examination.

The hymen, regarded in an anatomical point of view, possesses no peculiarity or speciality by which it is essentially distinguished from many like structures in other parts. It belongs to the same class of formations as the valvulæ conniventes of the intestines, and the frill-like folds of mucous membrane which not infrequently surround the terminal orifices of mucous tubes. In the fœtus such folds are seen with various degrees of distinctness at the termination of the urethra, vagina, and often of the rectum. The lower end of the vagina, in the fœtus *invariably* terminates in a marked projection outwards of the mucous lining of the tube. It takes the form of a laterally compressed conical fold, the base of which is continuous all round with the vaginal walls, but the apex is directed forwards. Its centre exhibits a vertical slit-like orifice, the direction of which is apparently due to the lateral compression of the nymphæ and labia, between which it lies. This is the hymen. In advanced fœtuses it is scarcely distinguishable in form, and only to a certain extent in size, from the similar conical termination of the cervix uteri, which projects into the vagina, as the hymen does between the nymphæ. The vaginal portion of the cervix uteri and the hymen both constitute invaginations or intussusceptions at two different points of the same mucous tube, —the one marking the division between the uterus and the vagina, the other between the latter and the external parts. The chief difference between them is that the direction of the orifice in the former is transverse, and in the latter vertical.

Such is the condition of the hymen during fœtal and infantile life. But as growth advances the posterior half becomes much more developed than the anterior, just as the posterior half of the uterus, the posterior lip of the cervix, and the posterior wall of the vagina, are commonly larger and more developed than the corresponding anterior halves. Thus it happens that in adults the hymen presents usually the form of a crescentic or semilunar fold, the concave border of which is directed upwards or forwards, while that which had been in the fœtus, the upper half, has now become unfolded or lost among the plaits of mucous membrane, situated at the upper part of the vaginal entrance. This, because it is the most constant, has been usually regarded as the typical form of the hymen. But the fœtal form is also often retained, namely, the circular fold of mucous membrane, which, as the parts become more expanded, acquires a round rather than a slit-like aperture. If, however, the folds of the mucous membrane lining the vagina are profusely developed, then the hymen also exhibits the form not so much of a distinct membrane as of an irregularly constricted orifice, the sides of which are puckered or gathered into plaits, so as nearly to close the vaginal entrance. And this also is a very common condition of the part, especially in young subjects.

The varieties, therefore, in the hymen which anatomists recognise, such as the crescentic, circular, cribriform, and the like, become easily explicable. They all proceed apparently from a common starting point, but differences in the degree of development, or accident, may determine the permanent form. The *half-circle* and *crescent* result from a normal development of the posterior, and a corresponding retrocession of the anterior, moiety of that conically projecting mucous fold which is more or less distinct in every fœtus. The hymen with a *central* or nearly central circular orifice, results from a flattening down and retiring within the vaginal orifice of the cone; the retiring naturally following upon an expansion of the vaginal walls as growth advances. The appearance of a *notched margin* to the central aperture is produced by the prominent edges of the terminal vaginal folds, which are in some subjects more profusely developed than in others. The *cribriform* hymen probably results from an abnormal cohesion of these notched edges, in such a manner, that small apertures are left between them, and the completely *imperforate* hymen by an entire adhesion of the margins of the orifice, the result sometimes of inflammation in infancy.

The hymen, however various its forms may be, consists of a double layer of mucous membrane, containing between its laminæ a small quantity of fibrous tissue and blood-vessels. It is of variable degrees of thickness, being in some subjects very strong and tough, and in others forming a very slender lamina. Its situation is at the entrance of the vagina. Although the depth at which it is placed within the vulva varies in different subjects, according to the thickness of the labia, and the size of the nymphæ and vestibule. Occasionally, as already stated, one or more plicæ of the vaginal mucous membrane, more than usually developed, form constrictions at a higher point within the canal, but the term hymen cannot with propriety be applied to any of these.

The presence of the hymen, although it raises a strong probability of virginity, yet affords no certain evidence upon that point, nor does its absence establish the contrary.

The hymen is commonly said to be ruptured on the occasion of a first complete intercourse, but the expression unfolded would probably, in many instances, more accurately represent the mode of its disappearance. Whenever the hymen presents any considerable membranous surface, doubtless a real laceration occurs, but in the cases in which it takes the form of a crescentic fold, or of a puckered rosette, instead of being lacerated, it probably becomes unfolded or flattened out, and so disappears, just as the ordinary vaginal folds are obliterated, by frequent intercourse or by parturition, without any rupture.

Upon the presumption that the hymen is always *lacerated* a certain hypothesis has been raised, namely, that the little fleshy bodies occasionally observed near the orifice of the vagina, termed *carunculæ myrtiformes*, constitute the remains of that membrane. But, notwithstanding a great amount of evidence that has been collected regarding the myrtiform bodies, it cannot be shown that these are anything more than accidental and uncertain formations, having nothing necessarily to do with the hymen.

The hymen may be broken by accident, or may become obliterated by the frequent employment of vaginal injections, and in other like modes. Or, from constant leucorrhœa, the parts may become so relaxed that a distinct membranous fold can be no longer discerned at the vaginal orifice, although there may have been no loss of virginity.

On the other hand, impregnation may take place without destruction of the hymen, which has frequently been found entire at the time of labour, and even in women affected by syphilis.*

Sebaceous and Muciparous Glands and Follicles of the Vulva. — The *sebaceous* follicles correspond with the male preputial follicles. They are scattered over the nymphæ, clitoris, and inner surface of the labia. Their secretion contains butyric acid and has a strong and somewhat ammoniacal odour. This occasionally becomes highly irritating, especially when cleanliness is neglected.

The *muciparous* follicles are arranged in groups, the principal ones being situated upon the vestibule (*vestibular follicles, fig.* 480. *v*), around and upon the sides of the meatus urinareus (*urethral follicles, fig.* 480. *u*), and at the sides of the entrance of the vagina (*lateral follicles of the vaginal orifice, fig.* 480. *va*).

The muciparous follicles are composed of a delicate vascular mucous membrane arranged in the form of short mucous crypts, or consist of simple or branched tubules ending

* In a case of extensive syphilitic periostitis which came under my notice, in a woman thirty years of age, who had previously been a prostitute, a tough membranous circular hymen closed the orifice of the vagina so completely that the tip of the fore finger could scarcely be inserted within it.

in a *cul-de-sac*. The vestibular follicles are of the former kind and the urethral of the latter.

All these vulvar follicles secrete a viscid mucus, the quantity of which becomes considerably increased under excitement or irritation. It serves to lubricate the several parts of the vulva.

The *vulvo-vaginal glands*, termed also the glands of Bartholin and of Duvernay, consist of two conglomerate glands of the size of a haricot bean, variable in form, and of a pale reddish yellow colour, which are placed one upon each side of the vagina near the entrance (*fig*. 480. *g*). They are lodged beneath the superficial perineal fascia, having their inner side united to the vagina by areolar tissue, and their outer surface in relation with the constrictor muscle of the vagina. The lobules composing this gland send off tubules which at its upper and fore part unite to form an excretory duct that proceeds horizontally forwards as far as the vaginal orifice, upon the side of which it terminates just within the nymphæ and externally to the hymen. The orifice of the duct (*d*) is covered by a falciform fold of mucous membrane, which renders its discovery sometimes difficult.

This gland secretes a viscid fluid resembling somewhat the prostatic fluid and having a peculiar odour. Under excitement its secretion is rapidly formed and, like the contents of the salivary duct, is sometimes emitted in a jet. This gland is probably homologous with Cowper's gland in the male. In infancy and early life it is very small, attaining its full development in the adult, and again diminishing and even disappearing in old age.

When the labia and nymphæ are abscised a series of vascular erectile structures are brought into view, which, together with a special muscle, surround the vaginal orifice. These are the *vestibular bulb*, *pars intermedia*, and *constrictor vaginæ muscle*.

Pars intermedia.—From the dorsal vein of the clitoris (*fig*. 481. *d*) several branches (*n*,*n*) pass downwards round the sides of the organ to communicate with a double row of closely-set venous canals, which commencing anteriorly at the glans extend backwards to the root of the clitoris in the form of a frill that completely occupies the angle contained in the curvature of the organ (*fig*. 481. *m* and *fig*. 482. *f*). These venous canals enter the body of the clitoris by a double row of apertures along its under surface. They represent the communicating veins between the corpus spongiosum urethræ and the corpora cavernosa penis. After receiving branches from the glans clitoridis (*fig*. 481. *l*), nymphæ (*r*), and labia (*p*), they form on either side a series of convoluted veins (*k*), which spreading downwards and outwards ultimately terminate below in the bulb of the vestibule (*fig*. 482. and 483. *a*). This is the structure termed by Kobelt the *pars intermedia*. It corresponds with the corpus spongiosum urethræ of the male, which in the female remains divided into two halves. The arteries of this structure (*fig*. 481. *q*) are derived from the pudendal.

Fig. 482.

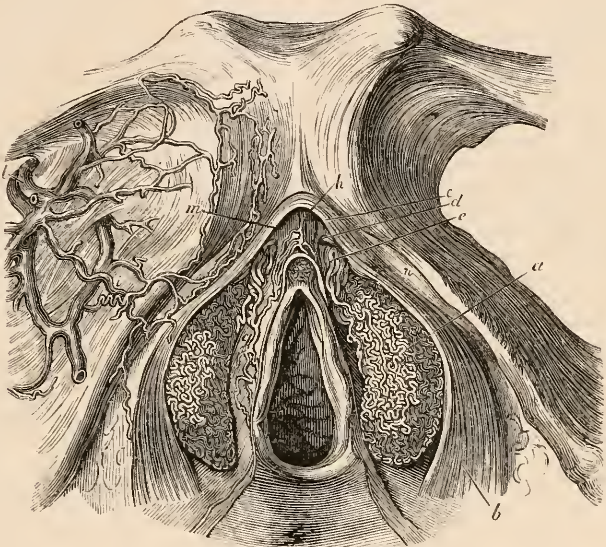
Lateral view of the forepart of the pelvis, attached to which are the clitoris and the vascular and erectile structures connected with it. (*After Kobelt.*)

a, vestibular bulb of the left side; *b*, veins passing off from the lower and posterior border of the bulb, to the pudendal vein; *c*, similar veins communicating with the hæmorrhoidal; *c'*, the spot at which the veins of the vestibular bulb pass off to the vagina; *d*, pars intermedia; *e*, glans clitoridis; *f*, ascending communicating veins proceeding to the body of the clitoris; *g* and *i*, lateral communicating branches between the vena dorsalis clitoridis and pars intermedia; *h*, vena dorsalis; *k*, bend of the clitoris; *l*, crus clitoridis; *n*, vulvo-vaginal gland.

Bulbus vestibuli (Kobelt). *Plexus retiformis v. reticularis* (De Graaf). *Crura clitoridis interna* (Swammerdam). *Plexus cavernosus* (Tabarranus). *Corpus cavernosum* (Santorini). *Semibulb* (Taylor). *Bulb of the vagina*.—Lying one on either side of the entrance to the vagina, and behind the nymphæ and labia, are two masses of vascular parenchyma, composed almost entirely of tortuous veins enclosed in a fibrous membrane. These in their collapsed state are of the size and form of an almond; but when injected may be compared to a filled leech (*fig*. 482. and 483. *a*). Anteriorly they are directly continuous with the structures last described, while from their sides communicating branches pass back to the obturator veins (*fig*. 483. *l*), and from their lower ends to the pudendal and hæmorrhoidal veins (*fig*. 482. *b* and *c*). The bulb of the vagina, now commonly regarded as the homotype of the bulb of the urethra which is here bipartite, forms the principal portion of the erectile tissue surrounding the vaginal orifice.

Constrictor vaginæ.—The clitoris together with its bipartite pars intermedia and vestibular bulb is encased in a thin sheet of muscular structure (*fig*. 483. *b* and *c*), which has been usually regarded as the constrictor of the vaginal orifice, but which Kobelt considers to be more particularly employed as a compressor of the parts just named. This muscle takes its origin in a broad flattened base (*b*) from the perineal fascia midway between the anus and tuber ischii. The inner fibres interlace with those of the sphincter ani, while the outer ones reach to the corresponding ascending ischial ramus. Thence the muscle becomes gradually smaller as it ascends, and after embracing the entire length and breadth of the vestibular bulb, it converges forwards to meet its fellow at the clitoris, where it terminates in two little flattened portions of which the posterior passes as a narrow tendon (*fig*. 483. *d*) to unite with its fellow between the upper end of the bulb and the root of the clitoris, while the anterior looser portion (*c*) mounts over the dorsum of the clitoris, forming the *musculus attrahens clitoridis*. This serves to depress the organ and compress the dorsal vein, at the same time that the lower portion of the same muscle, by compressing the rest of the vascular apparatus, forces the blood out of the vestibular bulb and pars intermedia upwards into the body of the clitoris, and thus aids in producing congestion and erection of all these parts during coition.

Fig. 483.



Anterior view of the parts represented in Fig. 482. (*After Kobelt.*)

a, vestibular bulb; *b*, constrictor vaginæ muscle, according to Kobelt the compressor of the bulb. It is here represented as drawn back behind the bulb, which in the natural position is covered by it. *c*, anterior division of the muscle which passes over the body of the clitoris, serving to depress the organ, and to compress the dorsal vein; *d*, posterior tendinous division of the same muscle; *e*, pars intermedia; *f*, glans clitoridis; *g*, veins proceeding from the nymphæ; *h*, dorsal vein of the clitoris; *i*, branches communicating with the obturator veins; *k*, branches ascending to the epigastric veins; *l*, obturator veins; *m*, corpus clitoridis; *n*, crus clitoridis of the left side.

Blood-vessels of the external organs. — The *arteries* are supplied by the terminal branches of the internal pudics and from branches of the femoral.

The pudic sends off two branches: the first, or lower (*superficial perineal branch*), terminates in the labium after supplying the sphincter vaginæ and some of the perineal muscles. The second, or superior, mounting along the ischio-pubic rami to the division of the crura clitoridis, sends off a branch (*artery of the bulb*) to the bulbus vestibuli, and then separates into two terminal twigs, the one (*profunda branch*) entering the cavernous substance of the clitoris, while the other forms the *dorsal artery* of that body (*fig*. 481. *h*).

The femoral supplies the *external pudics*, two in number on each side, which arise by a common trunk or singly from the inner side of that vessel. The superior of these branches (*superior pudenda externa*) arises near the crural arch and, passing inwards, sends off two branches, one to the mons veneris and lower part of the abdominal integuments, the other, terminating in the labium, sends also twigs to the nympha and preputium clitoridis. The inferior branch (*inferior pudenda externa*), arising a little below the former, or from the profunda, passes obliquely towards the labium in which it terminates, anastomosing also with the superficial perineal branch of the pudic.

Veins.—The veins of the clitoris and the venous plexuses surrounding the vaginal orifice, together with their communicating branches, have been already described. The *external pudic veins*, collecting the blood from the mons veneris and the interior of the labia, take a course similar to that of the corresponding arteries, and empty themselves into the saphena.

The lymphatics of the external organs terminate in the inguinal glands.

The nerves.—The external parts are abundantly supplied with nerves derived chiefly from the pudic. The pudic nerve arising from the lower part of the sacral plexus passes through the sacro-sciatic foramen and accompanying the pudic vessels divides into two branches.

The *inferior, or perineal branch*, sends twigs to the labia, nymphæ, and roots of the clitoris, and then gives off the *superficial perineal branch*, which is distributed to the constrictor muscle of the bulb of the vagina.

The *superior, or branch of the clitoris*, corresponds with the dorsal nerve of the penis. Beneath the pubic arch it passes between the roots of the clitoris and is distributed along the side of that organ in the manner already described (*fig.* 481. *i i*). Some of its ramifications are distributed upon the prepuce and in the nymphæ and upper parts of the labia.

The labium also receives nerves from the branches of the *inferior pudendal* nerve, a division of the small sciatic nerve. These communicate with the superficial perineal branches.

Abnormal Anatomy of the External Organs.

Labia.—The labia, together with the whole of the external generative organs, may be deficient, or they may retain through life an undeveloped or fœtal condition, consisting only of a very narrow fold of integument. In rarer cases, the labium of one side only has been developed. The labia may, on the other hand, present the form of a double or even a triple fold. In cases of deficiency of the lower part of the abdominal integument and anterior wall of the bladder, with separation of the pubic symphysis, the labia are imperfectly formed, and are set wider apart than usual, inclining somewhat outwards. The labial commissure is then also deficient. The posterior commissure of the labia may be much hypertrophied, projecting unusually forward, and covering more or less the entrance to the vagina. The labia are occasionally so completely coherent along the median line, that the vulvar fissure is obliterated, leaving only an aperture sufficient for the passage of urine. This condition is commonly the result of inflammation of the vulva in early infancy.

The diseases affecting the tissues of the labia may be superficially seated, or may involve more or less their entire substance. The principal superficial affections are erythematous inflammations, often accompanied by vesicular, chiefly herpetic or eczematous, and sometimes pustular eruptions; enlargement of the follicles, increased secretion, occasionally watery, and in excessive quantity, occurring in combination with a solid œdematous condition of the part (oozing tumour of the labium), excoriations, aphthous or specific (chancrous) ulcers; and condylomata, especially of the softer and syphilitic kind. The deeper seated affections are acute, and chronic inflammation of the fibrous and cellular tissue; induration and hypertrophy, sometimes of considerable extent (*elephantiasis*); serous infiltration, associated with pregnancy, or cardiac disease; suppuration producing large collections of pus within the labium; sloughing and gangrene. The veins of the labia frequently become varicose in multiparæ, and hæmorrhagic effusions take place into their substance. These effusions may be produced during straining efforts, or by external violence, but are especially apt to occur during labour, from pressure of the child's head upon the veins returning the blood from the venous plexuses that surround the vaginal orifice, whereby the latter become over-distended and ruptured, a considerable interstitial hæmorrhage often resulting. Cysts enclosing a glairy fluid, and adventitious growths of a more solid kind, such as are common to fibrous and cellular tissue, are not unfrequently found within the labia. Cancerous degeneration is more rare, but it may occur, either alone, or in combination with vaginal or uterine cancer. The labia may suffer laceration during labour, from forcible violation of the person, and in other ways. Fistulæ, communicating with the rectum, and permitting the passage of fœcal and gaseous fluids, occasionally form in the labia as sequelæ of suppurative processes. Lastly, these parts are occasionally the seat of hernia of the intestine, and, more rarely, of the ovary.

Clitoris.—Entire absence of the clitoris probably seldom or never occurs alone. But the clitoris and nymphæ may be deficient even when the labia are present. The clitoris is sometimes so small that its presence may escape detection. More often it is of unusual size, projecting beyond the labia. Such enlargements, though occasionally occurring without degeneration of the tissues, are more commonly the result of inflammatory hypertrophy, or are occasioned by profuse condylomatous (syphilitic) growths, in which the prepuce also may be included. The clitoris is also subject to cancerous degeneration, sometimes attaining an enormous size.

Nymphæ and vestibule.—The protrusion of the nymphæ between the labia, which occurs as a normal condition in infants, is not unfrequently observed in adults, when these parts, exceeding their ordinary dimensions, hang down below the posterior commissure: their lower extremities may in rare cases be prolonged as far back as the anus. The number of the nymphæ may be increased to two (Morgagni), or even three pair (Neubauer). Excessive hypertrophy of the nymphæ is common in certain climates. It may be associated with corresponding enlargement of the clitoris. The nymphæ are subject to the same inflammatory and specific disease as the labia, but they more commonly affect the surfaces than the substance of these parts, which, being of a denser texture than the labia, are not so easily infiltered with the venous, sanguineous, or puriform fluids, that readily collect within the latter.

The morbid conditions of the *vestibule* consist chiefly in inflammatory hypertrophy of the vestibular follicles, especially of those which immediately surround the urethral orifice and line the sides of the ostium vaginæ. They present the appearance of small red granulations. A more decided spongy vascular growth often springs from the border of the urethral orifice, where it forms either a bright red fringe, or a soft tumour, varying in size from a pea to a cherry (vascular tumour of the meatus). The vulvo-vaginal gland and its duct may be the special seat of blennorrhœa, sometimes of an infecting kind. This may be made to ooze from the orifice of the duct, by pressure behind the labium.

The most frequent varieties in the conditions of the *hymen and ostium vagina* have been already noticed.* The vaginal orifice may be nearly or completely obstructed by an adventitious membrane, or by the hymen preternaturally developed. Some of these states are congenital, but others are acquired. In either case, attention is often not called to them until after the establishment of puberty. According to their degree, they interfere with the functions of the vagina, partly or altogether preventing intromission, and rendering insemination imperfect or impossible. They impede the exit of the products of conception and the escape of the menstrual fluid. In the latter case, when menstruation is established, the fluid collects in and dilates the vagina and cervix uteri, and lastly the body of the uterus, and even the Fallopian tubes. Spontaneous rupture of the hymen, or membrane, may then occur, liberating the fluid.

PLACENTA.

The placenta is the organ provided in each pregnancy for the nutrition and respiration of the fœtus. To this it is connected on its free side by the umbilical cord, while its opposite or attached surface is united to the fundus, sides, or lower part of the body of the uterus by a layer of the decidua. A placenta exists only in the mammalia and in some of the cartilaginous fishes. It is composed of structures derived partly from the ovum and partly from the uterus. The fœtal or embryonal portion is not always furnished by the same portion of the ovum. It is sometimes constructed from the yolk sac, as in certain sharks, and the vessels which ramify in it are then the branches of the omphalo-mesenteric artery and vein. In other cases, as in the mammalia, the chorion supplies the fœtal portion, which is here rendered vascular by the umbilical vessels derived from the allantois. The maternal or uterine portion of the placenta is furnished by the decidua or lining membrane of the uterus. These two portions, viz., the fœtal and the maternal, originally distinct, and, even in their subsequent union, preserving a certain independence, become more or less closely connected together by interdigitating the one with the other. Their union may be one of mere contact, the fœtal portion forming numerous projecting vascular folds which in the form of laminæ or tufts, or single villi, are received into corresponding depressions or sulci, equally vascular, formed in the lining membrane of the uterus. Or it may consist in a more intimate conjunction of these parts, such as takes place in man, where the decidua or maternal portion forms a lamina which is spread over and united to the groups of villi that constitute the fœtal portion. In the former case at the time of parturition the two portions are separated, the fœtal processes being simply drawn out of the recesses which contained them without laceration of either of the tissues. But in the latter, the one part cannot be expelled without carrying a considerable portion of the other with it.

Form. — The mammalian placenta exhibits numerous varieties of form. In most Ruminants it is composed of numerous detached placentulæ constituting groups or bosses of vascular villi that project from the surface of the chorion, and are received into corresponding cotulæ upon the inner surface of the uterus. In the Carnivora the placenta encircles the fœtus in the form of a broad flat belt. In Pachydermata, Cetacea, and many other families, the villi are nearly evenly distributed over the whole surface of the chorion, so that the fœtus is everywhere surrounded by placenta. In some Rodentia and Quadrumana the placenta is double.

In man the placenta forms a single discoid organ, which in its natural position is slightly convex upon the outer, and concave upon the inner superficies. Its outline is generally *circular* or *oval;* it is sometimes *reniform*, *cordate*, or more or less *triangular*. It is rarely *bilobed* or *multilobed*.

Dimensions and weight. — The size of the placenta is exceedingly variable, bearing usually a certain proportion to the bulk of the child. A full-sized oval placenta measures 7—7½″ in its shorter, and 8—9½″ in its longer diameter, and measures 23—24″ in circumference. The thickness is generally greatest opposite to the point of entrance of the funis, where the organ measures commonly 1—1¼″, but it becomes gradually attenuated towards the margin, which is slightly rounded, measuring here only 2—4‴ in thickness. The weight of the placenta ranges from 15—30 oz. or more.

Fœtal surface.—Upon the fœtal surface of the placenta are observed portions of the amnion and chorion, together with the root of the funis and the principal branches of the umbilical arteries and vein.

Amnion.—The amnion (*fig.* 484. *am*), after furnishing the outer covering of the funis,

* See VAGINA and HYMEN.

passes off in all directions at the root of the cord, and spreads in a thin opaline lamina over the fœtal surface of the placenta, to which it slightly adheres. In some cases, especially when the umbilical vessels divide before entering the placenta, the amnion has no attachment at all to the latter. The amnion of the placenta does not differ in any respect from the rest of the amniotic sac, of which the placental portion constitutes about one third. Upon its fœtal surface is a single layer of flattened polygonal cells filled with delicate fat granulations.

Chorion. — The same proportion of chorion as of the amnion, namely, about one third of the entire superficies, is appropriated to the placenta. This, however, is not, like the amnion, simply an apposed membrane. It enters into the composition of the organ, and gives strength to it (*fig.* 484. *ch*). It sustains and transmits the branches of the umbilical vessels (*v f*), which adhere to, and ramify upon, its fœtal surface, between it and the amnion. This face of the chorion is united to the amnion by a thin and easily separable layer of soft pulpy tissue, constituting a portion of the *tunica media* of the ovum, while the reverse surface, which forms, as it were, the base or floor of the placenta, bears the numerous tufts or villi that make up the bulk of this organ.

Fœtal blood-vessels. — The blood-vessels of the placenta which belong to the fœtus are branches of the two umbilical arteries, and of the single umbilical vein. These, as just stated, ramify in large trunks over a considerable portion of the fœtal or under surface of the placenta, before they penetrate the chorion to gain the interior of the organ. When the fœtal vessels have been injected from the funis, their course upon this surface of the placenta is easily traced. Within the root of the cord, and at a distance of one inch from its insertion, the two umbilical arteries communicate together by a cross branch half an inch in length. Immediately on reaching the placental surface, each artery bifurcates, the branches passing off in opposite directions. A second bifurcation takes place, in the same manner, about half or three quarters of an inch from the first. And lastly, a third, at distances ranging from one to two and a half inches. Each of these dichotomous divisions is at first more or less abrupt and opposite, the vessels afterwards bending, and taking a slightly divergent or parallel course, or even somewhat approximating. After the third bifurcation, the vessels again divide and subdivide, but now at acute angles ; their extremities become lost, when they are reduced to the size of a crow quill, by dipping down suddenly, and passing through the chorion, to enter the substance of the placenta at distances varying from an inch to an inch and a half from its border. A small branch, however, in continuation, often runs on nearly to the edge. Lateral branches, of the same size as the terminal subdivisions, also leave the main vessels in all parts of their course, and dip down into the placental substance.

The branches of the veins, about sixteen in number, which return the blood from the interior of the placenta, emerge from its substance close to the points of entrance of the arteries, and take a less tortuous course than the latter. They, however, accompany these vessels, but more in the form of radiating lines, which proceed towards the root of the funis, passing under the arteries, and ultimately uniting in the single umbilical vein.

The varieties in the form of the placenta already noticed are apparently dependent upon certain modifications in the development and arrangement of these vessels, which are likewise very variable, although the same primary divisions are noticeable in all. In the *circular* placenta the root of the cord is inserted into, or near, the centre. In the *oval* form it is attached to the smaller extremity forming the *placenta en raquette*. In the *reniform* and *cordate* placenta, the insertion is likewise more or less lateral. Lastly, when the vessels of the cord divide before arriving at the surface, they form the *placenta en parasol.*

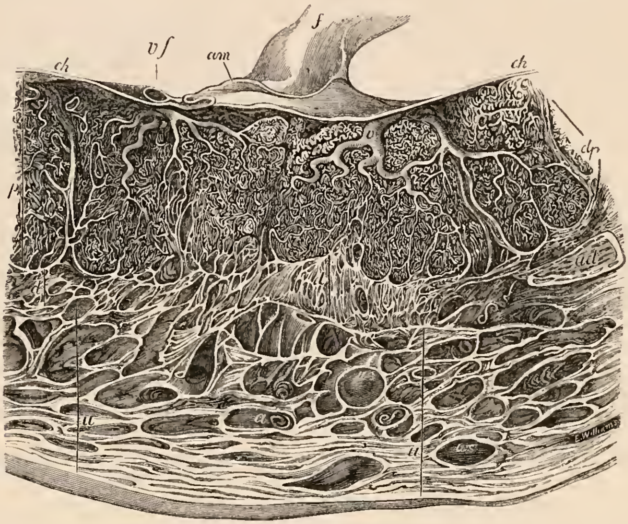
Uterine surface. — The reverse or uterine surface of a placenta which has been separated from its attachment, as in natural labour, is rough, and is divided into numerous rounded oval or angular portions, termed lobes or cotyledons. These vary from half an inch to an inch and a half in diameter. The whole of this surface consists of a thin, soft, and somewhat leathery investment of deciduous membrane, which dips down in various parts to form the sulci that separate the cotyledons from each other. This layer is a portion of the decidua which, as long as the parts are *in situ*, constitutes the boundary between the placenta and the muscular substance of the uterus, but which at the time of labour becomes split asunder, so that while a portion is carried off along with the placenta, and constitutes its external membrane, the rest remains attached to the inner surface of the uterus. This layer serves as a medium by which the uterine arteries (*fig.* 484. *a a*) and veins pass from the uterus into the placenta. Numerous valve-like apertures are observed upon all parts of the surface. They are the orifices of the veins which have been torn off from the uterus. A probe passed into any of these, after taking an oblique direction, enters at once into the placental substance. Small arteries, about half an inch in length, are also everywhere observed embedded in this layer. After making several sharp spiral turns, they likewise suddenly open into the placenta. These are the uterine vessels, which convey the maternal blood to and from the interior of the placenta.

Circumference. — The margin of the placenta is bordered all round by the united membranes which enter into its composition. Here the amnion and chorion, after lining the fœtal or concave surface, come into contact with the decidua which covers its uterine face, and the three membranes then pass off together to enclose the liquor amnii and fœtus. At this part the decidua is always most dense.

Partly within its substance is formed an incomplete sinus, the circular vein or sinus. This constitutes an interrupted channel, which more or less encircles the placenta. Several orifices are observed in its walls. Some communicate directly with the interior of the placenta, and others with the uterine sinuses.

Substance.—When a clean section has been made through the placenta (*fig.* 484.), the two surfaces already described are observed to enclose between them a soft spongy substance, which is made up principally of countless ramifications of the fœtal villi. These are attached at their base to the chorion, from

Fig. 484.



Vertical section of the walls of the uterus with the placenta attached. From a woman in the thirtieth week of gestation. (After Wagner.)

The length of the lines *u u*, serves to distinguish the uterus; *p*, the placenta, and *d d*, the decidua. To the right of the figure the decidua is separated into *ud*, uterine decidua, and *dp*, decidual prolongations which form the dissepiments dividing the placenta into lobes; *f*, funis; *am*, amnion; *ch*, chorion; *v f*, fœtal blood-vessels (divided) upon the surface of the placenta; *v v*, villi; *u s*, uterine sinuses; *a a*, curling arteries in the substance of the uterus.

which they spring, while their opposite extremities are united to the decidual layer forming the uterine boundary of the placenta. The interspaces left between the villi and their ramifications form what have been termed the cells of the placenta. They are widest between the roots of the villi, and much smaller between their extremities. In these spaces the maternal blood circulates. When injections are thrown into the placenta from the uterine arteries or veins, these spaces become filled, and the mass, when broken, exhibits a peculiar granular appearance. Dipping down among the villi, and reaching in some cases as far as the fœtal surface of the placenta, are numerous sheet-like prolongations of decidua (*fig.* 484. *dp*). These constitute the dissepiments which separate the entire mass into its several lobes or cotyledons. At the placental margin, the decidual layer generally dips under the villi, forming a return end or border, which is directed inwards, and is attached at a distance of 3—4‴ from the margin to the outer surface of the chorion. The exact relation of the decidua to the villi, in various parts of the placenta, will be better understood after a more minute description has been given of each of these structures.

The tufts and villi. — A placental tuft has been often compared to a tree. It consists of a trunk giving off numerous branches, which ultimately end in finer subdivisions or villi (*fig.* 484. *v v* and *fig.* 485. *a*). The trunks may be said to take root in the chorion, from which they spring, while the branches and finer subdivisions spread laterally and upwards, until they come into contact, at their sides, with the adjacent tufts and villi, and above with the decidua which bounds the placenta towards the uterus. Many of the villi, instead of branching like trees, proceed thread-like from the floor to the roof of the placenta, only sending off short knotty side branches. The tufts are so closely set, that their forms cannot be readily discerned until they are floated out in water. The stems are tough and fibrous, or coriaceous, while the branches and finer villi, though strong, are of a more brittle texture. When one of these is broken off, and examined by the microscope, it presents the following characteristics — the subdivisions are abrupt, contorted, and singularly devoid of symmetry; from all parts of their surface spring numerous short pullulations, which render them knotty and uneven.

Every villus is composed of two distinct parts, viz. an outer leathery sheath, and an inner softer and vascular structure, which is contained within the former like a finger encased in a glove. The distinction between these two structures is not easily observed, except in parts where the outer sheath has been accidentally broken off, leaving the more pulpy internal substance exposed. Or in cases where the placenta has become stale by keeping for a few days, when the inner portion by shrinking has retired from the end of the villus, so that a small interspace has been here left (*fig.* 485. *b*).

When a terminal tuft so prepared is viewed by transmitted light, under slight compression, the outer case is seen to consist of a transparent non-vascular structureless membrane, embedded in the substance, or attached to the inner surface of which are numerous flattened spheroidal cells, forming generally a single layer. In the apex of a growing tuft, or forming a distinct bud projecting from its extremity, may be often observed a group of similar cells which appear to be passing off from a spot in the centre of the mass.* These cells perform important parts in the growth and offices of the villi, which will be presently noticed.

The internal portion (*fig.* 485. *b*) consists of a soft and pulpy structure which envelopes the blood-vessels of the villi. In its substance also are embedded numerous cells of a similar nature to those observed in the structureless sheath.

Termination of the fœtal vessels. — The arrangement and terminal divisions of the blood-vessels within the villi varies considerably according to the age of the placenta. The following distribution is observed from the third to the sixth month (*fig.* 485. *a*). Each villus contains one or more arteries and veins, together with numerous capillaries. The arteries pass up the centre of the stem, and divide into branches according to the number of the terminal subdivisions. Within these the branches split up into numerous capillaries, which present various forms of arrangement, in some parts resembling Malpighian bodies, and in others the arrangement of pulmonic capillaries. From these capillaries the blood is collected by veins which pass back through the tufts accompanying the corresponding arteries. All these vessels, with their subdivisions, are enveloped and supported by the pulpy granular substance that forms the interior of every villus (*fig.* 585. *b*).

Towards the end of pregnancy, the true capillaries of the villi gradually disappear, so that in a placenta at term the blood-vessels present the condition accurately described by C. H. Weber and Goodsir. A single vessel generally enters each terminal tuft, and after forming an open loop, it returns again, either dividing within the villus, or leaving it as it entered. Or a single vessel may enter, and retire from two or more villi, before it terminates in a principal vein. Many modifications occur in the forms of the loops, which may be simple, compound, wavy, or much contorted, and in parts varicose.*

Fig. 485.

a, terminal villus of a fœtal tuft, from a placenta of six months. The arteries, veins, and capillaries are minutely injected. The latter, which disappear towards the end of gestation, are here very abundant. The arteries and veins occupy the centre, and the capillaries the surface, of the tuft, immediately beneath the non-vascular sheath. The nucleated non-vascular sheath is shown at *b*, separated from the internal softer structure in which the vessels ramify. (*Ad Nat.*)

Such, then, are the structures belonging to the fœtus which are brought into contact with the maternal blood in the interior of the placenta, viz. the portion of chorion that forms the floor of the placenta, and the tufts or villi which spring from its surface. The office of the former is simply mechanical in confining the maternal blood to its proper course, and preventing rupture of the organ; the latter constitutes the potential portion of the placenta.

On the other hand, the sole parts belonging to the mother, the existence of which can be anatomically demonstrated in the substance of the placenta, are formed out of the decidua.

The decidua.—A general description of this membrane, as it forms the roof of the placenta, and sends off dissepiments into its substance, has been already given. It only remains to

* J. Goodsir. Anatomical and Pathological Observations, 1845.

* These are the only terminations of the fœtal vessels of the placenta which have been hitherto described. The true capillary system disappears towards the end of gestation, and apparently, on this account, has escaped the attention of observers, as far as I am aware, except Schrœder van der Kolk, who, in his recent work, has described and figured them in a placenta of three months. Scanzoni also (Lehrbuch der Geburtshilfe, *fig.* 99.) reproduces the figure of Meckel and Gierse, in which the capillaries have evidently been injected; but this is given as an example characteristic of a dropsical placenta, and not as representing a normal state.

explain the exact relations of this structure to the villi, within the placenta. All the extremities of the villi which are sufficiently long to reach across the placenta from the chorion to the opposite surface formed by the decidua, become firmly attached to the inner side of the latter. This attachment takes place not by any actual perforation of the decidua, but by the ends of the villi being simply inserted, in an early stage of the formation of the placenta, into little shallow pits or cup-like depressions in the decidual substance, into which they are received, and from which they may be withdrawn.* In other cases, the ends of the villi become blended with the decidua, to which they are apparently fixed, by a growth of decidual cells. These attachments are for the purpose of giving strength to the placenta, and of mechanically supporting the villi. They take place not only between the ends of the villi and the decidua forming the roof of the placenta, but also wherever decidua and villi come into contact. Hence similar attachments are also formed between the villi and the septa or dissepiments (*fig.* 484. *d p*), which divide its substance into separate lobes. Upon the floor also of the placenta all round the margin, where the decidua turns downwards and inwards to become united with the chorion, and to form the placental margin, the decidua is found for a short distance attached to the bases of the villi. And this arrangement gives to the parts an appearance as if the decidua had been here penetrated by the villi, but one which is actually occasioned by the former having, in the course of growth, become extended around the roots of the latter long after these were first formed. Occasionally also decidual cells may be found upon the surface of villi, connecting together their extremities, or forming here and there rough irregular belts upon their stems.

Termination of the maternal vessels. — No extension of the maternal blood-vessels into the substance of the placenta among or between the villi, can be demonstrated to take place. So far as anatomical evidence goes, the maternal vessels all terminate at once and abruptly upon the inner surface of the decidua. The curling arteries, after passing from the muscular coat of the uterus, obliquely for the most part, through the layer of decidua which forms the roof of the placenta, open directly into the interior of the latter; while the veins commence by equally abrupt openings which conduct through the decidual layer to the venous sinuses in the uterine walls. These venous orifices occupy three situations. The first and most numerous are scattered over the inner side of the general layer of decidua which constitutes the upper boundary of the placenta; the second form openings upon the sides of the decidual prolongations or dissepiments, which separate the lobes from each other; while the third lead directly into the interrupted channel in the margin, termed the circular sinus.

Development of the placenta. — The early steps in the formation of the placenta have been described in the account which has been already given of the development of the *decidua* during gestation (p. 653.). These first steps consist in the formation out of the decidua of a perfectly spherical chamber, in the centre of which lies the impregnated ovum.

The surface of the ovum is at this time covered everywhere by short club-like villi of equal size. The extremities of these villi are simply in contact with, but are not as yet attached to the walls of the containing chamber. Subsequently both the villi and the decidua forming the fœtal chamber undergo considerable metamorphoses. Certain portions of these become intimately united, in order to form the placenta; while other portions suffer retrogression, and take no part in its construction. The following are the principal features in these metamorphoses.

Fœtal portion. — The surface of the ovum does not long retain the peculiarity just mentioned, of being equally covered by villi. During the second month at least, if not earlier, those villi on the side furthest from the uterus cease to grow, and in consequence of the increasing expansion of the ovum become more widely scattered over this part of its surface, while those nearest to the uterus rapidly increase in size and extent, so that this portion of the ovum soon exhibits a profuse growth of villous processes, which send out their ramifications in all directions.

According to Professor Goodsir, the development and growth of the villi proceed from the groups of cells already described as occupying their bulbous extremities. These swellings on the sides and ends of the villi are their germinal spots, and are the active agents in the formation of these parts. The villus elongates by the addition of cells to its extremity, the cells passing off from the germinal spot, and the spot receding on the extremity of the villus, as the latter elongates by the additions which it receives from it.

As the villi increase in size, their strength is gradually augmented by the conversion of the membrane and cells forming their stems and larger branches into a tough white fibrous texture; while frequently, towards the end of gestation, calcification is observed to begin within the finer villi, and to proceed sometimes to so great an extent that a considerable number of them become filled up and obliterated by solid matter. While these changes are going on in the outer portion of the villi, or

* The difficulty of understanding the early steps in the construction of the placenta has arisen from the belief commonly prevalent, that the ovum on first reaching the uterus remains upon the outside of the decidua, and that the villi of the chorion penetrate its substance or enter the uterine glands in order to form the placenta. But there is no actual penetration of the decidua at any period, except that which consists in the *entire* ovum gaining a situation in the interior of this membrane shortly after its arrival in the uterus. The *tips* of the villi at a certain stage, as above described, become superficially imbedded in the walls of the fœtal chamber, which is formed of decidua; but this is not a penetration of the decidua, as commonly understood, but only a means of fixing the ovum.

that which is derived from the chorion, important modifications occur in the interior structures. Up to a certain period of gestation, the chorion and its villi contain no blood-vessels. According to the author last quoted, blood-vessels first appear in these parts when the allantois reaches and applies itself to a certain portion of the interior surface of the chorion. The umbilical vessels then communicate with the substance of the villi, and become continuous with loops in their interior. Those villi in which the blood-vessels do not undergo any further development, as the ovum increases in size, become more widely separated, and lose their importance in the œconomy. The villi, again, in which vessels form, in connection with the umbilical vessels, increase in number, and undergo certain changes in the arrangement of their constituent elements. As the blood-vessels increase in size, the cells diminish in number, but are always found surrounding the terminal loop of vessels in the situation of the germinal spot.

The injections of Schrœder van der Kolk * show a profusion of capillaries within the villi as early as the third month. And at later periods of gestation, up to the sixth month, I have succeeded without difficulty in displaying, by the aid of fine injections, such an abundant development of these vessels, as is exhibited in *fig.* 485. Before the end of gestation, however, the greater part or all of these fine capillaries have disappeared, and the vessels within the villi then show only the long tortuous varicose loops which Goodsir has so well described.

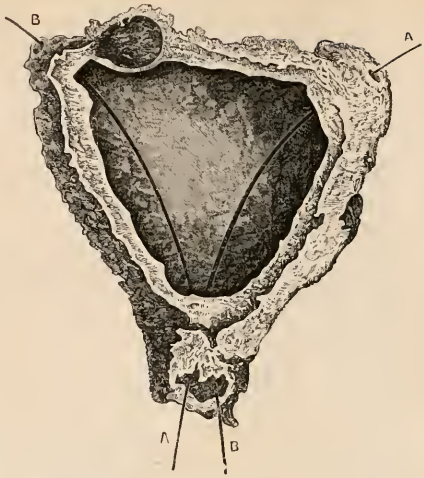
Such are the principal modifications which normally take place during the development and growth of the fœtal portion of the placenta. The changes occurring in the maternal portion, or that which is supplied by the decidua, are not less remarkable.

Maternal portion. — Four principal stages may be observed in the formation of this portion of the placenta.

The first stage is that in which the decidua constitutes a perfectly spherical chamber † surrounding the ovum, but having as yet no structural connection with it (*fig.* 486.). This is the condition of the ovum in the early part of the first month of gestation.

The second stage is marked by the commencing attachment of the villi all round to the inner surface of the containing chamber, so that now the ovum becomes fixed, and can no longer be turned out, except by breaking off the villi, or drawing out their ends from the little pits, or anfractuosities, already described in the walls of the decidua, in which they have become embedded. At this period (latter half of the first month), the decidua forming the walls of this chamber is sufficiently firm to admit of dissection, and already there may be traced, upon its inner surface,

Fig. 486.



Decidua at the beginning of gestation, exhibiting the fœtal chamber in the first stage of its formation. The ovum, being at this time unattached, has dropped out of it. (*After W. Hunter.*)

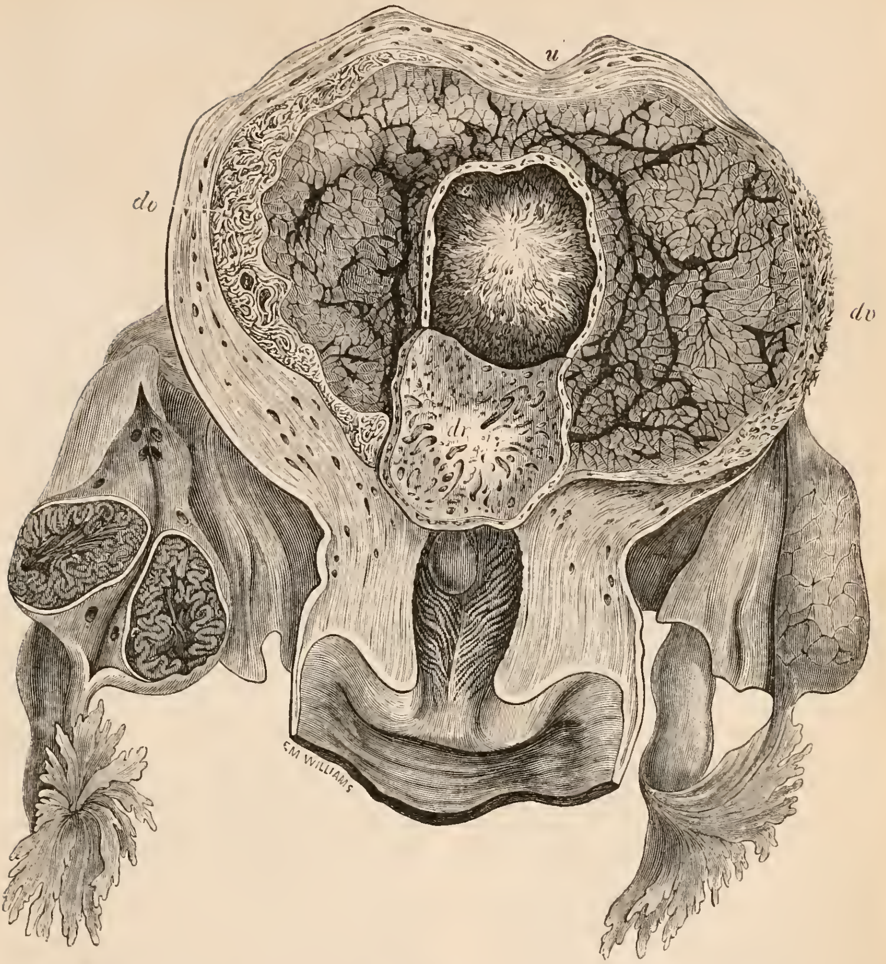
orifices communicating with canals in the decidua that lead into the uterine sinuses. The maternal blood already flows freely into the fœtal chamber, and, after passing everywhere among the villi, is returned into the uterine veins. Thus a *temporary placenta* is formed, which, as in Pachydermata, Cetacea, &c., entirely surrounds the ovum (*fig.* 487.).

The third stage is the most important. It marks the transition from the temporary to the permanent form of the placenta. Coincidently with the increased development of the villi on one side of the chorion, and their corresponding arrest of growth on the opposite surface, there occurs an increase of the space between the decidua and the ovum on one side, and a corresponding decrease of it upon the opposite side. The increase is always on the side next the uterus, where the villi are most abundant, and the decrease upon the opposite surface, where they are fewest. And this change continues progressively, until, upon the bald side of the ovum, the decidua reflexa and the chorion come into so close contact that the interspace is obliterated, and the blood, which formerly flowed freely among the villi, is now no longer admitted to this part of the circumference of the ovum ; while, upon the side which is directed towards the uterus, a large space is left which now takes the form of a meniscus. In order more effectually to confine the blood within this limited space, an increased development of decidual cells now takes place, which pass off from the uterine walls, and attach themselves to the chorion all round the circumference of this space, and thus is formed the margin of the permanent placenta. During all this time, the ovum, by its growth, has been gradually raising the decidua above and around it, just as the common integument becomes raised dur-

* Loc. cit. pl. i. *fig.* 1.

† For an account of the formation of the fœtal chamber, and of the early steps in the construction of that portion of the placenta which belongs to the decidua, see p. 653.

Fig. 487.



The formation of the fœtal chamber more advanced than in fig. 486. *The ovum is still evenly covered by villi, the ends of which, about this time, begin to be attached to the walls of the chamber in which the ovum is contained.*

o, ovum; *d r*, decidua reflexa, forming the fœtal chamber; *d v*, decidua vera; *u*, uterine walls.

ing the formation of a subcutaneous abscess; while in proportion as the base of the chamber becomes extended by the gradual retiring, from the centre, of the line of reflexion of the decidua, like waves receding from a central point, so, at the same time, an increasing surface is produced by the expansion of the uterus itself; and the layer of decidua here formed, commonly termed the decidua serotina, is simply the mucous membrane reproduced to supply the place of that which had been consumed or pushed off in forming the decidua reflexa.

The fourth or final stage consists in the partitioning of the permanent placenta into smaller portions or lobes by the extension of the layer of decidua (serotina) which lies opposite to the developed villi inwards at various points towards the chorion. In this way are constructed the dissepiments already described as bounding the several lobes or cotyledons. This partitioning of the placenta commences about the fourth month.

Thus, during these several stages in the formation of the placenta, two processes may be said to be concurrently carried on which tend in opposite directions — a process of positive enlargement and growth combined with one of relative retrogression or limitation. For while the bulk of the placenta is progressively increasing up to the completion of pregnancy, the relative amount of surface of the ovum appropriated to it is, on the other hand, diminished. The entire surface of the chorion being, in the first stages of development, employed as a placenta; while in the latter half of gestation, one third of it suffices for that purpose.

Functions of the placenta. — By means of the placenta, the blood of the mother is brought into mediate relation with that of the fœtus. Two currents, the one fœtal, and the other maternal, are continually flowing into and from this organ, yet in channels so perfectly distinct that no direct commingling of the streams can ever take place. Nevertheless, though no passage of the form-elements of the blood can occur, yet through the partition-walls which separate these two currents, all the materials necessary to the growth of the fœtus are conveyed by endosmotic processes, and all the changes necessary to the respiration of the fœtus, and to the elimination of effete materials, are effected. The mechanism by which these ends are accomplished is of two kinds. The one consisting of means for bringing the two constantly flowing streams of blood into juxtaposition, the other of instruments for carrying on the nutritive and eliminative processes which are the objects of this conjunction.

The fœtal blood conveyed by the branches of the two umbilical arteries, is distributed to the villi, whence, after being exposed, in the finer vessels and capillaries which ramify upon their inner surface, to the influence of the maternal blood, it is returned to the funis by the branches which terminate in the single vein. The propelling power by which the blood is moved resides in the heart of the fœtus, and the whole of its circulating fluid is thus carried in successive portions through the placenta.

The maternal blood, after having its impetus diminished by the spiral course which the arteries take in passing through the walls of the uterus, as well as through the decidua, is delivered at once into the placenta, where it becomes immediately separated into fine streamlets by the villi which are so closely set as to break up the interior of the organ into countless channels. After flowing everywhere among the villi, the blood escapes back into the uterine system * by the venous orifices upon the surface of the decidua, and upon the dissepiments and marginal furrows from which it is conducted, through the decidual coat, to the sinuses in the substance of the uterus, and thence is returned to the mother's body by the uterine and spermatic veins.

During the flow of these streams through the interior of the placenta, the surface of the villi is constantly bathed by the maternal blood. Nevertheless the blood of the fœtus is separated from that of the mother — first, by the walls of its own capillaries; secondly, by the gelatinous membrane in which these ramify; and thirdly, by the external non-vascular nucleated sheath derived from the chorion. With the latter alone, the maternal blood is brought into direct contact.

Each of these structures has its distinct office. The use of the external layer of cells (*fig.* 485. *b*) has been happily illustrated by Goodsir. They are to the ovum what the spongioles are to the plant: they supply it with nourishment from the soil in which it is planted. Thus their action is selective, and they transmit to the interior of the villus the materials necessary for fœtal growth. These again are taken up by the internal layer of cells (*fig.* 485. *b*), and by them brought into direct contact with the fœtal capillaries. By a similar process, the interchanges necessary to respiration are effected through the membranous surfaces which separate the maternal and fœtal blood. And these processes, respiratory and nutritive, are continued without intermission from the moment that the two separate currents are established until the final separation of the fœtus in the act of birth. Yet, throughout pregnancy, the form of the mechanism by which these changes are effected is continually altering, either in its greater or lesser parts. The greater changes have reference chiefly to mechanical, and the lesser to vital necessities. The changes in form exhibit a beautiful series of adaptations in the capacity and strength of the placenta to the increasing amount and force of the maternal current. The original plan of the placenta, that of an interspace between two spheres (a lesser one contained within a greater) filled by maternal blood, could not be long preserved with the materials out of which the temporary organ is constructed. For as the ovum grows, the decidua reflexa, which alone confines the blood

* I can arrive at no other conclusion than that the blood in the interior of the placenta, is as much external to the maternal vascular system as it is while passing through a quill inserted between the divided ends of a vein in a living animal. Although, in this belief, I find myself opposed to the views of Weber, Müller, J. Reid, Goodsir, and Schrœder van der Kolk, who, with certain differences maintain that the blood is still retained within the maternal system. The views of these and of many other physiologists, who more or less agree with them, are divisible into two classes. According to one view, the uterine vessels either form a network in the substance of the placenta (Weber), or become expanded into an enormous sac, composed of the inner coat of these vessels, which envelopes everywhere the surface of the villi (J. Reid), so that the blood after circulating within the placenta is returned to the uterus without having been extravasated. According to the other view (Goodsir and Schrœder van der Kolk), the decidua throws a close investment over every villus, and forms that outer covering of cells which I have ascribed to the chorion; so that in this view a lamina of uterine structure still separates the maternal blood from the exterior of the villi.

On this and other points relating to the minute structure and composition of the placenta, consult *Von Baer*, Untersuchungen über die Gefässverbindung zwischen Mutter und Frucht in den Saügethieren. 1828. *Ritgen*, Beiträge zur Aufhellung der Verbindung der Menschlichen Frucht mit dem Fruchthälter. 1835. *Sharpey*, in Müller's Physiology by Baly. 1837 and 1848. *Eschricht*, De organis quæ respirationi et nutritioni fœtus mammalium inserviunt. 1837. *E. H Weber*, in Hildebrandt's Anatomie, b. iv., and in *Wagner*, Elements of Physiology. 1841. *J. Reid*, Edinb. Med. and Surg. Journ., No. 146. *J. Dalrymple*, Medico-Chirurgical Trans., vol. xxv. 1842. *Goodsir. J.* and *H.*, Anatom. and Pathol. Observs. 1845. *Schrœder van der Kolk*, Waarnemingen over het Maaksel van de Menschelijke Placenta, en over haren Bloods-omloop. 1851.

that flows around it, becomes thinner, and finally gives way by extension. But long before this stage arrives, the whole of this portion is shut out from the maternal circulation, and the subsequent metamorphoses are directed to the strengthening of the more limited space which remains. It is on this account that the strong border of decidua is formed around the margin of the now restricted area. The base of the placenta now consists of the tough and resisting chorion; while that portion alone of the decidua which is strengthened externally by the uterine walls is retained to form the opposite boundary. Ultimately, as the current of maternal blood flows with increasing force into the placenta in proportion to the growth of the latter, this becomes subdivided by the decidual septa, which apportion the entire organ into separate placentulæ, and thus the larger supplies necessary to the increasing exigencies of the fœtus are disposed of without danger of rupture to any portion of the organ.

The changes in the more minute structures which belong to the fœtus are not less interesting. The profuse development of fine capillaries within the fœtal tufts, which is so conspicuous from the third to the sixth month, is connected not only with the functions of respiration and nutrition of the fœtus, but also with the growth of the villi themselves. But when the period of viability of the fœtus has arrived, the proportionate amount of capillary vessels within the villi becomes greatly reduced, until finally only the original stems of the vessels are left. And this relative reduction of the channels through which the fœtal blood flows, becomes more marked, until, as the time of birth approaches, many of the villi become more or less obliterated, and cease to admit blood, often in consequence of that calcareous degeneration which, from the frequency of its occurrence, may be regarded rather as a normal process significant of natural decay than as an evidence of any morbid or preternatural change.

The series of metamorphoses is closed by the degeneration of the materials which bind the placenta, and consequently the fœtus, to the uterus. The layer of decidua forming the connecting medium between the uterus and the fœtal structures, in common with the rest of this membrane, suffers slow disintegration, and its component cells are converted into molecular fat. And now the strength of the adhesion being gradually diminished, it only remains for the contractile power of the uterus to be evoked in order to accomplish the separation together of the fœtus and placenta, like ripe fruit detached from the parent bough.

The illustrations of this article marked, "ad naturam," are from original drawings and preparations in the possession of the author. For the rest of the figures the authorities are given.

The usual signs are employed: for an inch ″; for a line ‴; and for the amplification ×.

The following tabulated arrangement of the principal contents will facilitate reference to the several subjects, as well as to the books quoted in the foot notes of this article.

UTERUS AND ITS APPENDAGES.

(*Arthur Farre.*)

ANALYTICAL INDEX

TO THE

SUPPLEMENTARY VOLUME.

ANALYTICAL INDEX

TO THE

SUPPLEMENTARY VOLUME.

GENERAL INDEX

TO

THE CYCLOPÆDIA OF ANATOMY AND PHYSIOLOGY.

The following have been accidentally omitted from the General Index:

GENERAL INDEX.

The Arabic figures refer to the paging; the Roman numerals to the Volumes; and s. to the Supplementary Volume.

E.

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X.

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THE END.

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